# Subtropical Coral-reef Associated Sedimentary Facies Characterized by Molluscs (Northern Bay of Safaga, Red Sea, Egypt)

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## Summary

The shallow marine subtropical Northern Bay of Safaga is composed of a complex pattern of sedimentary facies that are generally rich in molluscs. Thirteen diver-taken bulk-samples from various sites (reef slopes, sand between coral patches, muddy sand, mud, sandy seagrass, muddy seagrass, mangrove channel) at water depths ranging from shallow subtidal to 40m were investigated with regard to their mollusc fauna >1mm, which was separated into fragments and whole individuals.

Fragments make up more than 88% of the total mollusc remains of the samples, and their proportions correspond to characteristics of the sedimentary facies. The whole individuals were differentiated into 622 taxa. The most common taxon, *Rissoina cerithiiformis*, represented more than 5 % of the total mollusc content in the samples. The main part of the fauna consists of micromolluscs, including both small adults and juveniles. Based on the results of cluster-, correspondence-, and factor analyses the fauna was grouped into several associations, each characterizing a sedimentary facies: (1) "*Rhinoclavis sordidula - Corbula erythraeensis - Pseudominolia nedyma* association" characterizes mud. (2) "*Microcirce* sp. - *Leptomyaria* sp. association" characterizes muddy sand. (3) "*Smaragdia* spp. - *Perrinia stellata - Anachis exilis* - assemblage" characterizes sandy seagrass. (4) "*Crenella striatissima - Rastafaria calypso - Cardites akabana* - assemblage" characterizes muddy seagrass. (5) "*Glycymeris spp. - Parvicardium sueziensis - Diala* spp. - assemblage" characterizes sand between coral patches. (6) "*Rissoina* spp. - Triphoridae - Ostreoidea - assemblage" characterizes reef slopes. (7) "*Potamides conicus - Siphonaria* sp. 2 - assemblage" characterizes the mangrove.

The seagrass fauna is related to those of sand between coral patches and reef slopes with respect to gastropod assemblages, numbers of taxa and diversity indices, and to the muddy sand fauna on the basis of bivalve assemblages and feeding strategies of bivalves. The mangrove assemblage is related to those of sand between coral patches and the reef slope with respect to taxonomic composition and feeding strategies of bivalves, but has a strong relationship to those of the fine-grained sediments when considering diversity indices. Reef slope assemblages are closely related to that of sand between coral patches in all respects, except life habits of bivalves, which distinctly separates the reef slope facies from all others.

## Introduction

Indo-Pacific molluscan studies are generally rare because investigations on ecology or facies distributions mainly focus on corals or coral communities. Moreover, most published molluscan studies concentrate on hard substrates and/or easily accessible intertidal areas (e.g., ARNOUD & THOMASSIN, 1990; AUSTIN et al. 1980; AYAL & SAFRIEL, 1981; FRANK, 1969; HADFIELD, 1976; KLEEMANN, 1990, 1992, 1995; LEE & MORTON, 1985; SAFRIEL et al., 1980; SCHUHMACHER, 1993; TAYLOR, 1971, 1976; TAYLOR & REID, 1984; ZUSCHIN & PILLER, 1997a, b, c).

Modern marine death assemblages in sediments comprise mostly molluscan remains (POWELL et al., 1989) and, in most sediments, molluscs comprise the most abundant and diverse of the geologically preservable macrofaunal remains (e.g., EKDALE, 1977). To date, however, only a few Indo-Pacific studies have treated the mollusc fauna of subtidal sediments (e.g., BANDEL, 1991a; KAY & SWITZER, 1974; MASTALLER, 1978; SHEPPARD, 1984; TAYLOR, 1968); to our knowledge none of the previously published studies dealt quantitatively with the total mollusc fauna of various sedimentary environments.

Molluscs and their fragments are by far the most dominant particles > 250 µm in the Northern Bay of Safaga, generally comprising more than 50% (PILLER & MANSOUR, 1990). They range third among sediment constituents of a thin-section analysis including all grain size fractions (PILLER, 1994). Most of the molluscs in our samples are "micro-

Address: Dr. M. Zuschin, Prof. Dr. J. Hohenegger, Geozentrum, Institut für Paläontologie, Althanstr. 14, A-1090 Wien; Fax: 0043-1-31336-784, E-mail: martin.zuschin@univie.ac.at
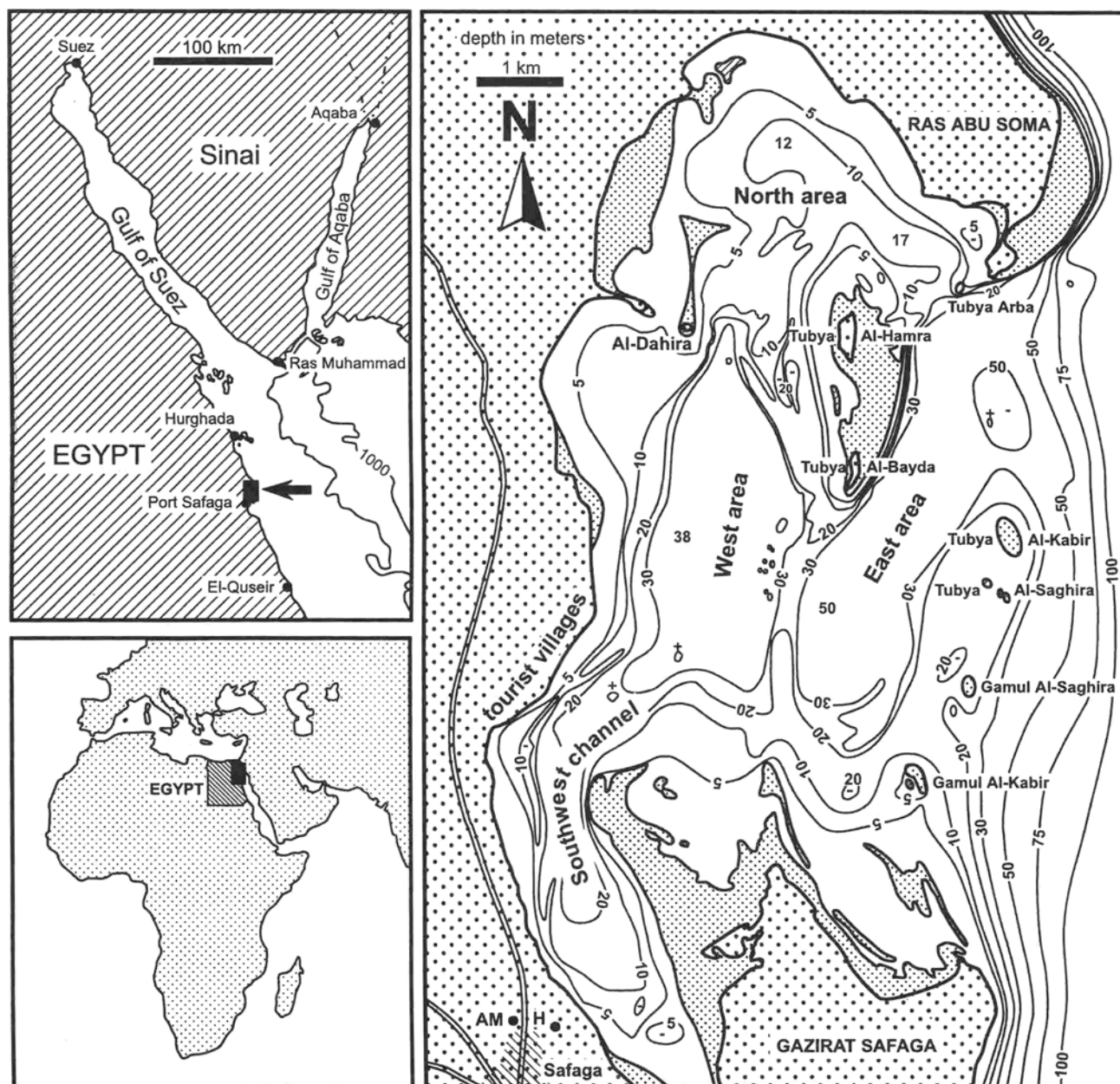
Fig. 1. Location map and general bathymetry of the study area (after Piller & Mansour, 1990). Dense stippled fields in the right map are intertidal areas. AM = Aerial mast, H = "Safaga Hotel".

molluscs", which we loosely define as adult individuals of small-sized species and juveniles of larger ones not exceeding 10 mm in greatest dimension (modified after Bandel, 1991a and Kay & Switzer, 1974). The main goal of this study is to investigate the potential of molluscs to characterize sedimentary facies and to extract facies-descriptive mollusc-associations from an enormous number of encountered taxa. A second important point is to test various taxonomic, ecologic and taphonomic assemblage features (individual numbers, numbers of taxa, numbers of fragments, diversity indices, feeding strategies and substrate relations) regarding their potential for facies description. Special emphasis will be placed on evaluating the preservation potential of the studied death assemblages due to the dominance of micromolluscs.

## Study area and sample locations

Within an integrated project in the Northern Safaga Bay (Red Sea, Egypt; Fig. 1), bottom facies (Piller & Pervesler, 1989), sediments (Piller & Mansour, 1990, 1994; Piller, 1994; Mansour et al., 1995), burrows (Dworschak & Pervesler, 1988) and organisms with considerable fossilization potential were studied. These include foraminifera (Haunold et al., 1997), corals (Riegl & Piller, 1997), coral-boring bivalves (Kleemann, 1990, 1992, 1995), coralline algae (Piller & Rasser, 1996; Rasser & Piller, 1997), echinoids (Nebelsick, 1992a, 1992b, 1995a, 1995b, 1996; Nebelsick & Kampfer 1994), and molluscs (Zuschin & Piller, 1997a, b, c).

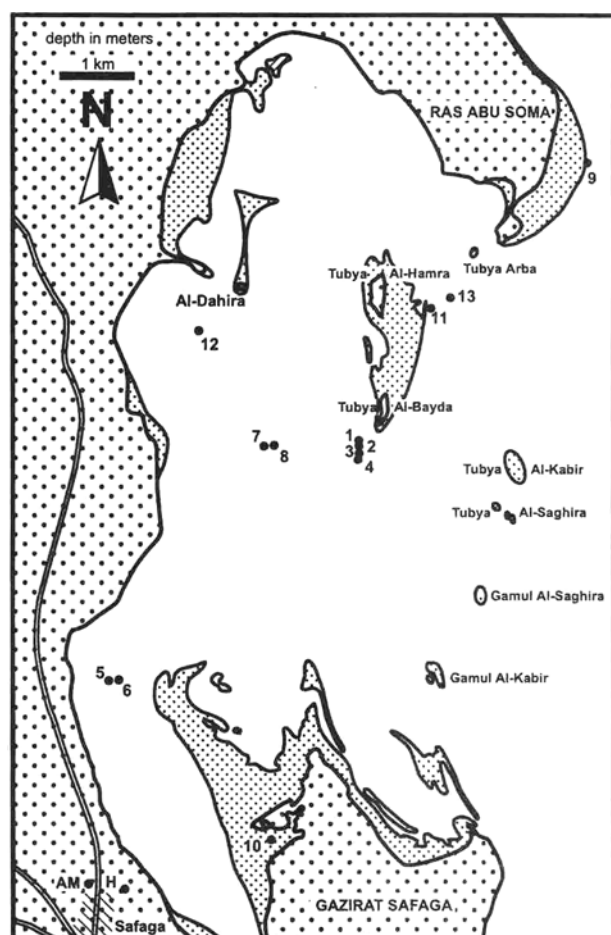The Northern Bay of Safaga is a shallow-water area

Fig. 2. Sample locations. AM = Aerial mast, H = "Safaga Hotel". See Table 3 for designation of facies

with highly structured bottom topography reaching down to more than 50 m (fig. 1). The annual water temperature ranges between 21 - 29°C, salinity between 40 - 46‰, both without any obvious depth gradient due to complete water mixing. The tidal range is < 1 m. Terrigenous (thus nutrient) input occurs mainly along the coast and is due to fluvial transport during flash floods, local erosion of impure carbonate rocks and aeolian transport by the prevailing northerly winds (PILLER & MANSOUR, 1994). Water energy is relatively weak, but a complex current pattern influences facies development (PILLER & PERVESLER, 1989)

and bottom facies and sedimentary facies generally show a good correspondence (PILLER & MANSOUR, 1990; PILLER, 1994). In this paper the terminology of sedimentary facies (PILLER & MANSOUR, 1990) is replaced by the terminology for bottom facies (modified after PILLER & PERVESLER, 1989), because the latter gives a better view on the origin of the samples and in most cases also provides information on sedimentological features (e.g. mud, muddy sand, sandy seagrass) (tab. 1).

All studied sedimentary facies except the mangrove channel are represented by more than one sample (tab. 1). In some sedimentary facies, samples were taken only a few meters from each other (mud, muddy sand, and sand between coral patches). In contrast the two samples from the reef slope and from seagrass come from completely different areas of the bay (fig. 2). The mud, muddy sand and sand between coral patches facies are very uniformly developed over wide areas of the bay; differences between these sedimentary facies are very well expressed by distinct differences in grain size distributions (PILLER & MANSOUR, 1990). Both seagrass samples come from areas dominated by the seagrass species Halophila stipulacea; in the shallower setting, Halodule uninervis and Cymodocea rotundata also occur in subordinate quantities. The two samples differ mainly in water depth (6m vs. 40m), grain size ("sandy" seagrass vs. "muddy" seagrass) and seagrass density (dense seagrass coverage in sandy seagrass vs. sparse coverage in muddy seagrass).

The two fringing reef samples come from areas with very different coral assemblages, steepness of the slope, and sedimentological features. The sample from Ras Abu Soma was taken on a very steep slope with comparatively high scleractinian diversity, dominated by Acropora spp. and the hydrozoan Millepora dichotoma among a variety of cooccurring faviid and poritid corals. The sediment is gravelly to sandy and very poorly sorted. In contrast the sample from Tubya Al-Hamra comes from a flat morphology with a clear dominance of Porites spp. The sediment is a comparatively well sorted sand.

The mangrove consists exclusively of Avicennia marina and the mangrove sediment is moderately to poorly sorted sand (PILLER & PERVESLER, 1989; PILLER & MANSOUR, 1990).

| sample no. | actual sample no. | water depth | bottom facies | sedimentary facies | microfacies |
|---|---|---|---|---|---|
| 1 | 94/1/a | 10m | sand between coral patches | coralgal facies | coralgal facies |
| 2 | 94/1/b | 10m | sand between coral patches | coralgal facies | coralgal facies |
| 3 | 94/1/c | 10m | sand between coral patches | coralgal facies | coralgal facies |
| 4 | 94/1/d | 10m | sand between coral patches | coralgal facies | coralgal facies |
| 5 | 94/3/a | 23m | muddy sand | molluscan facies | foraminiferan sand facies |
| 6 | 94/3/b | 23m | muddy sand | molluscan facies | foraminiferan sand facies |
| 7 | 94/4/a | 39m | mud | mud facies | mud facies |
| 8 | 94/4/b | 39m | mud | mud facies | mud facies |
| 9 | 94/5 | 19m | reef slope | coralgal facies | coralgal facies |
| 10 | 94/6 | <1m | mangrove-channel | terrigenous facies | terrigenous facies |
| 11 | 95/31 | 12m | reef slope | coralgal facies | coralgal facies |
| 12 | B5/8 | 6m | sandy seagrass | soritid facies | soritid facies |
| 13 | C1/3 | 40m | muddy sand with seagrass | molluscan facies | foraminiferan sand facies |

Tab. 1. Basic sample data: information on bottom facies slightly modified after PILLER & PERVESLER (1989), information on sedimentary facies after PILLER & MANSOUR (1990), information on microfacies after PILLER (1994).

## Material and methods

Thirteen standardized bulk samples of various sedimentary environments and bottom facies ranging from shallow subtidal to 40 m water depth were taken by scuba diving (fig. 2; tab. 1). A steel cylinder (diameter 35 cm) was pushed into the sediment and the uppermost 30cm, with a volume of 29 dm³ was collected into a 1mm - mesh net. The sediment was air-dried and molluscs > 2cm were removed before splitting the samples using a modified sample splitter as described by KENNARD and SMITH (1961).

Living molluscs were extremely rare and are estimated to contribute far less than 1% to the total mollusc content. Therefore the studied mollusc associations are treated as death assemblages (sensu KIDWELL & BOSENCE, 1991).

Whole shells > 1mm were used for facies analysis based on taxonomic composition. A whole shell is defined as having > 90% of the original form (DAVIES et al., 1990). Because it is not feasible to perform percentage measurements on the large amount of material, the 90% criterion was evaluated visually. Accuracy may be low, but precision is considered to be high because estimations were performed by one person only. Shells that did not match the 90% criterion were considered as fragments and excluded from the taxonomic part of the study for two reasons: 1) the enormous number of fragments in the studied size range made a practicable taxonomic treatment impossible. 2) For fragments, although of great taphonomic value (DAVIES et al., 1989a), in most cases a taxonomic identification was possible at the family level only, and would therefore reduce the taxonomic potential for recognizing sedimentary facies. For example, DAVIES et al. (1989a) were able to show that unbroken shells more accurately reflected the local fauna than did fragments. The fragments were counted however, and treated as taphonomic features of the studied sedimentary facies.

Disarticulated skeletal elements of molluscs, such as single valves of bivalves and plates of polyplacophorans, were treated as whole individuals for several reasons: 1) a consistent differentiation between left and right valves was not possible for the very abundant juvenile glycymerids, especially G. arabicus and G. lividus, 2) molluscs and their body parts were considered as sedimentary particles rather than "ecological individuals" for the facies approach, 3) the sample size is small relative to the size of the sampling domain and therefore counting each body part as a unique individual ("maximum likelihood estimate") is a very reasonable estimate of the number of unique individuals (for a detailed review of estimating individuals from body parts see GILINSKY & BENNINGTON, 1994), 4) maximum likelihood estimates are the most common methods of estimating the relative abundance of species in fossil assemblages (HOLTZMAN, 1979).

Bivalve identification is primarily based on OLIVER's (1992) Red Sea monograph. For gastropods no comprehensive monograph of Red Sea taxa is available, and their identification is therefore based on a large number of revisions of major taxonomic groups (e.g. HOUBRICK, 1992; BRATCHER & CERNOHORSKY, 1987; CERNOHORSKY, 1984) and monographs of various Indo-Pacific regions (e.g. KAY, 1979; SHARABATI, 1984; BOSCH et al., 1995). For scaphopod identification, SCARABINO (1995) was used; because it is difficult to identify the exclusively isolated polyplacophoran plates, an estimated number of 20 polyplacophoran species was summarized into one taxon. The quantitative treatment of molluscs is based on their abundance (number of individuals); statistical analyses were carried out with the SPSS 6.1.3 program package.
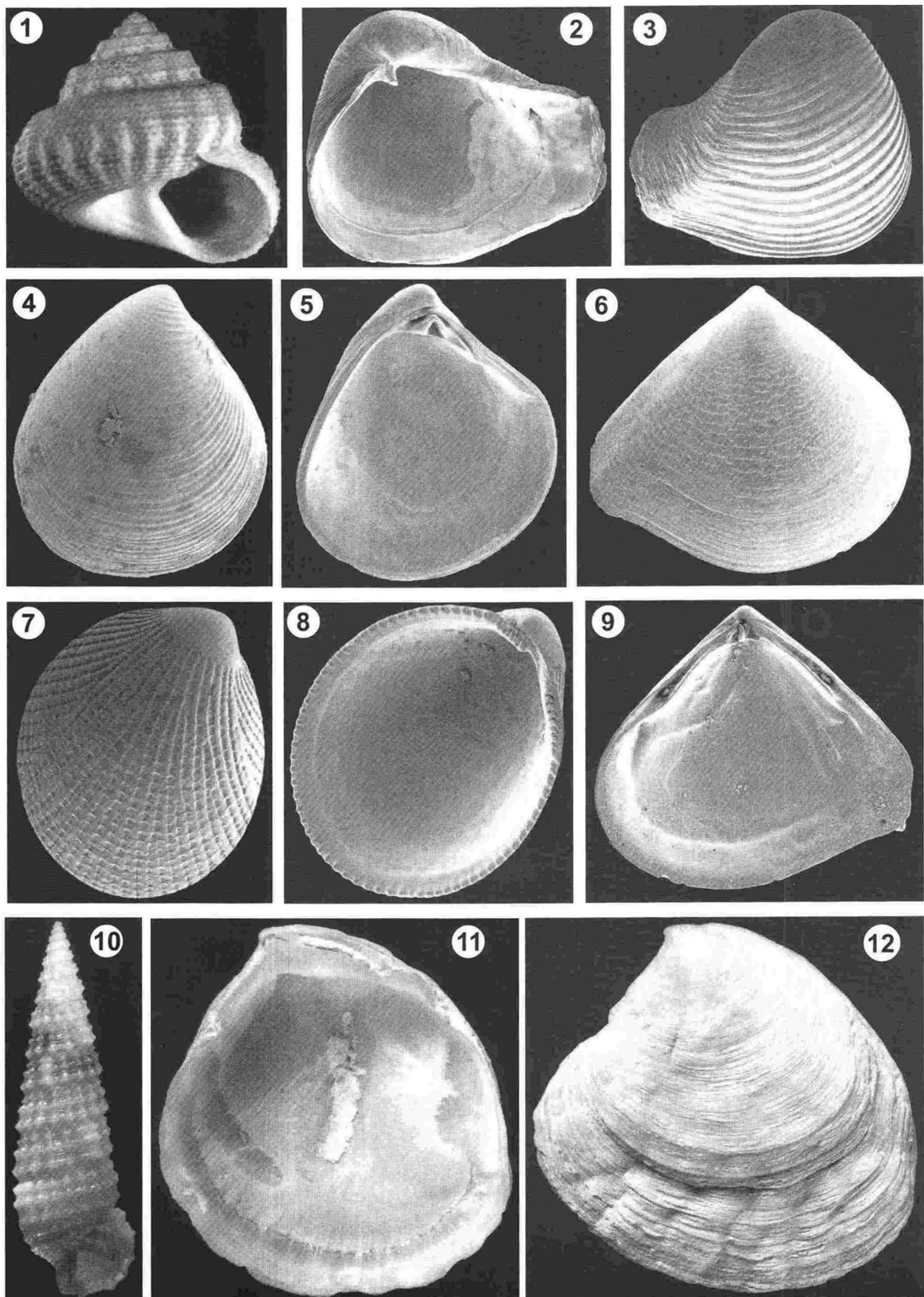
Diversity was measured in several ways. The Margalef-Index was used to quantify species richness (MAGURRAN, 1988). For heterogeneity we used the Simpson Diversity Index in comparison to the Shannon-Wiener function (MAGURRAN, 1988; KREBS, 1989). The latter index was also used to determine the evenness in frequencies between taxa within sites (PIELOU, 1969; KREBS, 1989).

Samples were grouped on the basis of taxa proportions using the 'Minimum Variance'-approach (WARD, 1963; ORLOCI, 1967). Transformation of proportions was performed using the arcsine-root method (LINDER & BERCHTOLD, 1976) to gain linear data, which are necessary for most hierarchical cluster analyses.

Cluster analyses on absolute frequencies of taxa were carried out with (1) combined bivalves, gastropods, scaphopods and polyplacophorans; (2) bivalves only; and

Plate 56   The most abundant character taxa of the studied assemblages in the Northern Bay of Safaga, Red Sea, Egypt

Fig. 1.   Pseudominolia nedyma, x 5.5
Fig. 2.   Corbula erythraeensis, right valve, internal view, x 12
Fig. 3.   Corbula erythraeensis, right valve, external view, x 13
Fig. 4.   Microcirce sp., right valve, external view, x 18
Fig. 5.   Microcirce sp., left valve, internal view, x 21
Fig. 6.   Leptomyaria sp. right valve, external view, x 26
Fig. 7.   Crenella striatissima, right valve, external view, x 29
Fig. 8.   Crenella striatissima, right valve, internal view, x 24
Fig. 9.   Leptomyaria sp. right valve, internal view, x 36
Fig. 10.   Rhinoclavis sordidula, x 5
Fig. 11.   Rastafaria calypso, right valve, internal view, x 2.5
Fig. 12.   Rastafaria calypso, left valve, external view, x 2.5

Plate 56                                                                                    233

%
21
19
17
15
13
11
9
7
5
3
1

reef slope
sample 9
22 taxa >1%=65.92%
155 taxa <1%=34.08%

%
21
19
17
15
13
11
9
7
5
3
1

reef slope
sample 11
21 taxa >1%=62.57%
212 taxa <1%=37.43%

Rissoina cerithiiformis
Zafrona isomella
Septifer sp.
Spondylus sp. juv.
Hyotissa sp.
Hipponix conicus
Plesiotrochus souverbianus
Hipponix sp. 2
Acar plicata
Polyplacophora
Pisulina adamsiana
Cerithium cf. zebrum
Triphoridae gen. et sp. indet. 1
Buccinidae gen. et sp. indet. 1
Barbatia parva
Patelloida profunda
Triphoridae gen. et sp. indet. 6
Chamoideagen. et sp. indet.
Cerithium egenum
Diala semistriata
Triphoridae gen. et sp. indet. 11
Stosicia sp.

Rissoina cerithiiformis
Ceritoturris sp.
Hyotissa sp.
Septifer sp.
Hipponix conicus
Polyplacophora
Diala semistriata
Wallucina erythraea
Tellina lactea
Zafrona isomella
Cerithium egenum
Limopsis sp.
Euplica ionida
Buccinidae gen. et sp.indet. 1
Gibberula sueziensis
Collonista arsinoensis
Plesiotrochus souverbianus
Acar plicata
Patelloida profunda
Zafra cf. selasphora
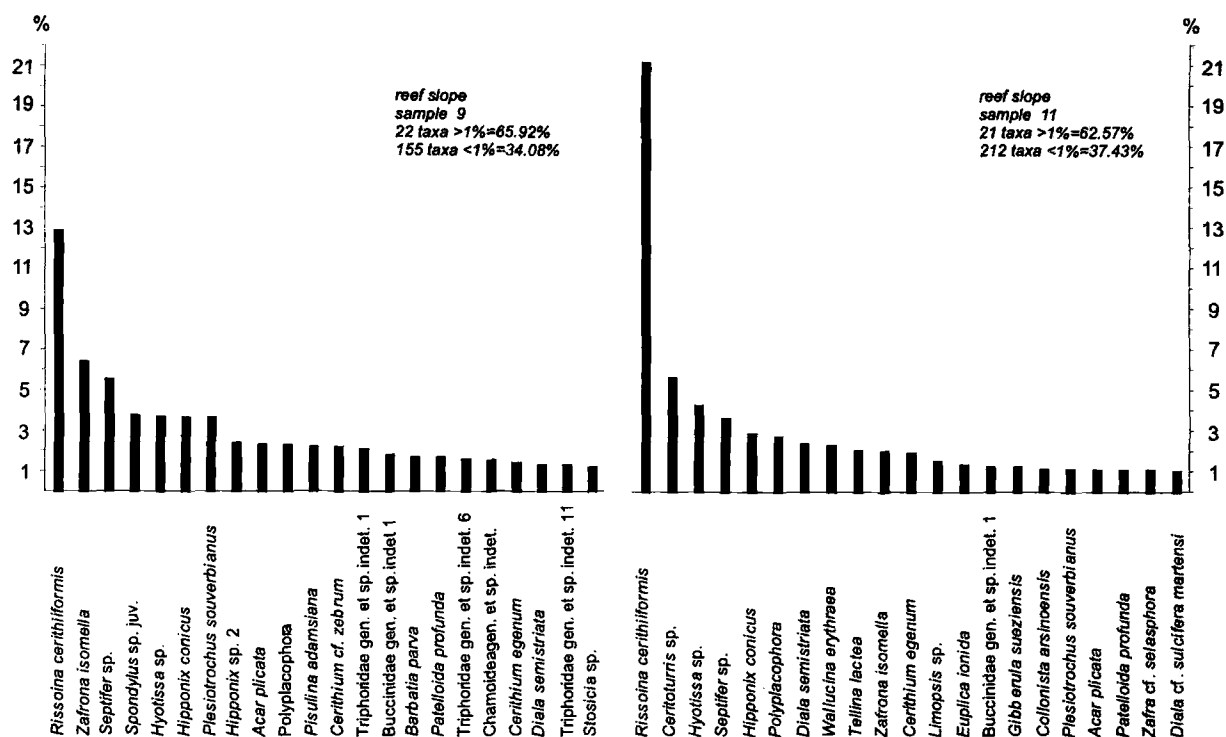Diala cf. sulcifera martensi

Fig. 3. Relative frequencies of taxa (complete data set) in samples from reef slopes.

(3) gastropods only. Both the complete and reduced sets were used for cluster analyses. Data reduction was carried out by (1) combining related taxa that could not be consistently distinguished because of poor preservation, (2) combining related taxa with similar distributions and (3) excluding taxa (and combined taxa) that contribute less than 1% to the content of at least one bulk sample. This treatment reduced the mollusc fauna used in the analysis from 622 to 96 taxa (tab. 7, tab. 9). Cluster analyses for the complete data set and for the reduced set yielded identical results. Additionally a cluster analysis using only the numbers of taxa was carried out.

In addition to cluster analyses based on taxonomic composition, three additional cluster analyses based on descriptive data and ecological data were carried out. These were based on (1) individual numbers of the four recognized molluscan classes; (2) standardized diversity indices (between 0 and 1); and (3) a simplified data matrix on feeding strategies and substrate relations of bivalves was used.

Because commonly used hierarchical cluster analytical methods create distinct, non-overlapping classes, they can be used to detect well-separated groups such as sites in a heterogeneous environment. Although clearly distinct classes of sites are recognized, their taxa may not show the same degree of distinctness. According to the Braun-Blanquet approach, associations are characterized by a few taxa, termed character taxa, which are restricted with

Plate 57    The most abundant character taxa of the studied assemblages in the Northern Bay of Safaga, Red Sea, Egypt

Fig. 1.    Cardites akabana, right valve, external view, x 32
Fig. 2.    Cardites akabana, right valve, internal view, x 29
Fig. 3.    Siphonaria sp. 2, x 12
Fig. 4.    Perrinia stellata, x 14.5
Fig. 5.    Glycymeris arabicus, left valve, external view, x 35
Fig. 6.    Glycymeris arabicus, left valve, internal view, x 35
Fig. 7.    Smaragdia souverbiana, x 14
Fig. 8.    Parvicardium sueziensis, left valve, external view, x 32.5
Fig. 9.    Parvicardium sueziensis, left valve, external view, x 36
Fig. 10.   Anachis exilis, x 18
Fig. 11.   Diala sp., x 37.5
Fig. 12.   Potamides conicus, x 26
Fig. 13.   Triphoridae gen. et sp. indet., x 19
Fig. 14.   Rissoina cerithiiformis, x 20.5
Fig. 15.   Ostreoidea (Hyotissa sp.), right valve, internal view, x 1
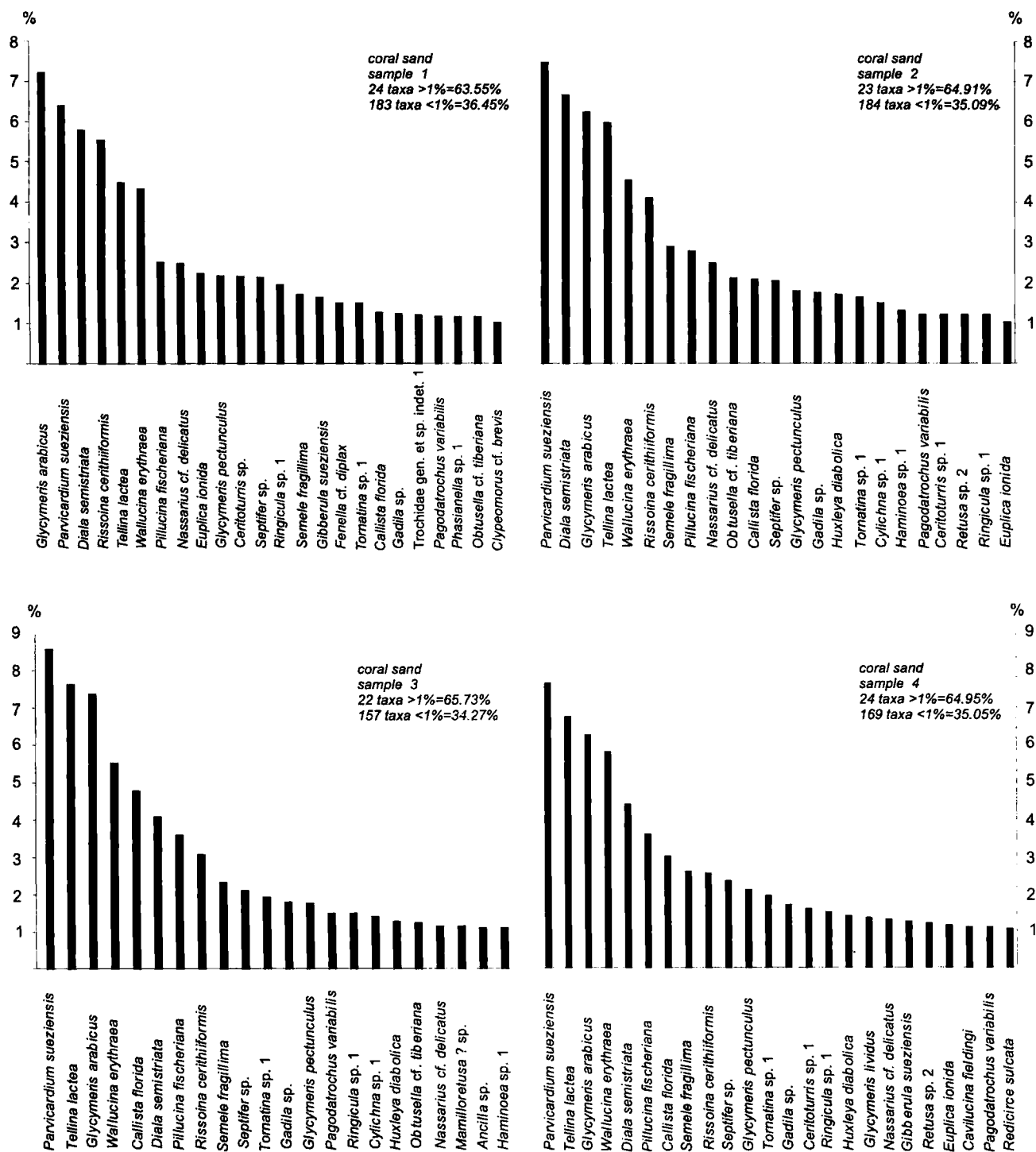
Plate 57 235
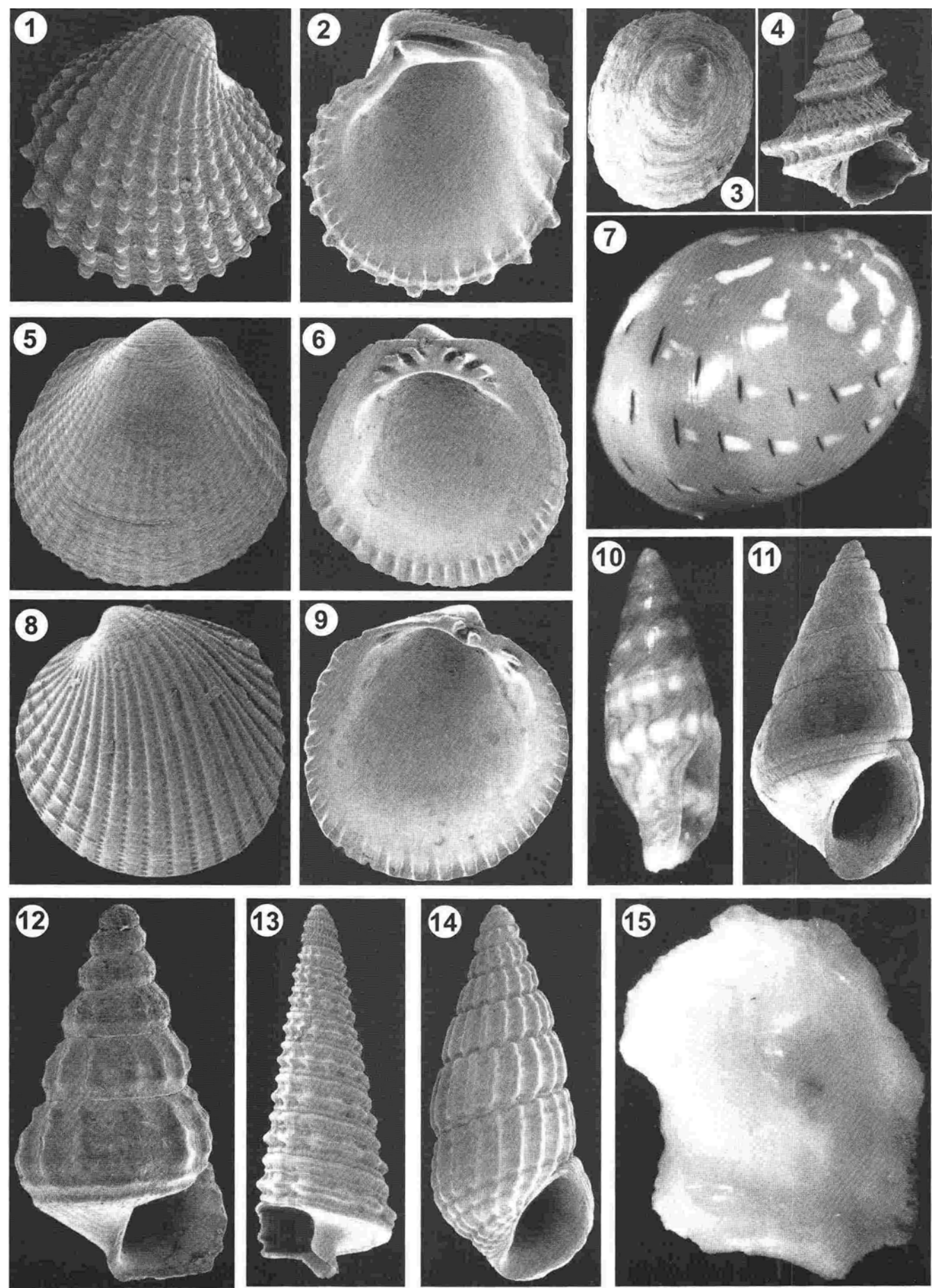
Fig. 4. Relative frequencies of taxa (complete data set) in samples from coral sand.

a high degree of fidelity to these associations (WESTHOFF & VAN DER MAAREL, 1973) but are not necessarily the prevalent taxa (e.g., CALEF & HANCOCK, 1974) or the trophic nucleus (e.g., WALKER, 1972; ANTIA, 1977; FÜRSICH, 1977). Most taxa within anyone association are present in other associations as well. These intermediate forms cannot be detected by non-overlapping cluster analyses. Therefore, ordination methods were used to clarify the relations between taxa and sites. Also, they may help to evaluate the reality of groups delineated by clusters. Because fre-

quency data are represented in a contingency table, correspondence analysis as an ordination method was used for data reduction (BENZECRI, 1973; HILL, 1973). The advantage of this method is the direct derivation of frequencies without transformations and the simultaneous representation of sites and taxa within the same system of axes in the form of biplots (GABRIEL, 1971).

In order to detect ecological and environmental factors, which cannot be directly observed, latent structure methods were developed (e.g. JÖRESKOG et al., 1976;

| taxon | % |
|---|---|
| 1 *Rissoina cerithiiformis* | 6.64 |
| 2 *Parvicardium sueziensis* | 4.68 |
| 3 *Diala semistriata* | 4.46 |
| 4 *Glycymeris arabicus* | 4.10 |
| 5 *Tellina lactea* | 3.96 |
| 6 *Wallucina erythraea* | 3.50 |
| 7 *Bellucina semperiana* | 3.14 |
| 8 *Septifer sp.* | 2.26 |
| 9 *Pillucina fischeriana* | 1.92 |
| 10 *Ceritoturris sp.* | 1.78 |
| 11 *Callista florida* | 1.65 |
| 12 *Semele fragillima* | 1.65 |
| 13 *Microcirce sp.* | 1.63 |
| 14 *Hyotissa sp.* | 1.29 |
| 15 *Nassarius cf. delicatus* | 1.24 |
| 16 *Glycymeris pectunculus* | 1.19 |
| 17 *Fenella cf. diplax* | 1.16 |
| 18 *Obtusella cf. tiberiana* | 1.12 |
| 19 *Tornatina sp. 1* | 1.11 |
| 20 *Hipponix conicus* | 1.03 |
| 21 *Euplica ionida* | 1.02 |
| 22 *Pagodatrochus variabilis* | 1.01 |
| 23 *Zafrona isomella* | 0.99 |
| 24 *Gibberula sueziensis* | 0.97 |
| 25 *Gadila sp.* | 0.94 |
| 26 *Ringicula sp. 1* | 0.91 |
| 27 *Huxleya diabolica* | 0.83 |
| 28 *Corbula erythraeensis* | 0.75 |
| 29 *Divaricella macandrewae* | 0.71 |
| 30 *Smaragdia rangiana* | 0.71 |

Tab. 2. The 30 most abundant taxa of the 13 bulk samples.

KRZANOWSKI & MARRIOTT, 1995). Factor analysis based on correlation matrix, with principal components as initial factor configuration, and subsequent varimax rotation, was performed on bivalve and gastropod abundance within sites, where the latter were treated as variables for factor extraction.

## Results
### Taxonomic composition

The 26382 whole individuals picked from 13 samples were assigned to 622 taxa. Most of the taxa are gastropods (444), followed by bivalves (171) and scaphopods (6). A

single species, *Rissoina cerithiiformis*, contributed more than 5 % to the total mollusc content of the 13 samples (tab. 2); only 22 taxa comprised more than 1 % (tab. 2); and only 151 taxa, more than 0.1%.

Looking at the individual samples reveals a rather distinct pattern of dominant species: *Rissoina cerithiiformis* strongly dominates the samples from reef slopes: it contributes nearly 13% to the sample from the *Acropora* - *Millepora* dominated reef slope, and more than 21% to the sample from the *Porites* dominated reef slope; all other taxa contribute less than 7% each to the total number of individuals in either of the two samples (fig. 3). The four samples from sand between coral patches are dominated by several taxa, with *Glycymeris arabicus*, *Parvicardium sueziensis*, *Diala semistriata*, *Tellina lactea* and *Wallucina erythraea* being among the most important; each of these taxa contributes less than 9% to each sample (fig. 4). The sample from sandy seagrass is strongly dominated by *Diala semistriata* (>13%) and *Bellucina semperiana* (>9%) (fig. 5), the sample from muddy seagrass by *Bellucina semperiana* (>18%), *Cardites akabana* (>13%) and *Divaricella macandrewae* (>7%) (fig. 5). All other taxa contribute less than 6% each to each of the two samples. The two samples from muddy sand are strongly dominated by *Bellucina semperiana* (>28% and >31%) and *Microcirce sp.* (>17% and 28%) (fig. 6); all other taxa contribute less than 8% to each of the two samples. The two samples from mud are dominated by *Rhinoclavis sordidula*, *Corbula erythraeensis* and *Pseudominolia nedyma* each of which contributes between 12 and 18% to each sample (fig. 7). The mangrove-sample is strongly dominated by *Potamides conicus* (>32%) (fig. 7).

The cluster analyses based on all taxa, on gastropods only and on bivalves only are nearly identical and correspond to a clustering of samples according to sedimentary facies (fig. 8). The grouping of mollusc associations at a higher hierarchical level reflects different relationships to the sedimentary facies: on the basis of bivalves, seagrass associations are similar to those of muddy sands and muds, whereas the gastropods of the seagrass association are similar to those of the reef slope and sand between coral patches. The mangrove association is distinct, with a close relation to the associations of the coarse-grained sediments (bivalves only) and seagrass (gastropods only).

The number of taxa is very high in the samples from reef slopes (2 samples), sand between coral patches (4),

| facies | | sand between coral patches | | | | muddy sand | | mud | | reef slope | | mangr. | seagrass | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 11 | 10 | 12 | 13 |
| number of taxa | bivalves | 66 | 62 | 53 | 63 | 38 | 36 | 26 | 32 | 47 | 55 | 23 | 47 | 60 |
| | gastropods | 135 | 140 | 140 | 125 | 44 | 43 | 37 | 48 | 129 | 177 | 46 | 107 | 104 |
| | scaphopods | 4 | 4 | 3 | 4 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 1 | 1 |
| | polyplacophora | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| | total | 206 | 207 | 197 | 193 | 84 | 81 | 65 | 82 | 177 | 233 | 70 | 155 | 165 |
| diversity indices | Margalef | 18.19 | 18.10 | 17.50 | 17.72 | 8.71 | 8.14 | 6.88 | 8.83 | 16.93 | 20.46 | 8.16 | 15.04 | 17.57 |
| | Simpson | 0.97 | 0.97 | 0.97 | 0.97 | 0.86 | 0.85 | 0.90 | 0.92 | 0.96 | 0.94 | 0.86 | 0.96 | 0.93 |
| | Information | 4.25 | 4.20 | 4.11 | 4.19 | 2.77 | 2.67 | 2.71 | 2.89 | 4.06 | 4.05 | 2.81 | 3.74 | 3.54 |
| | evenness | 0.80 | 0.79 | 0.77 | 0.79 | 0.52 | 0.50 | 0.51 | 0.54 | 0.76 | 0.76 | 0.53 | 0.70 | 0.67 |

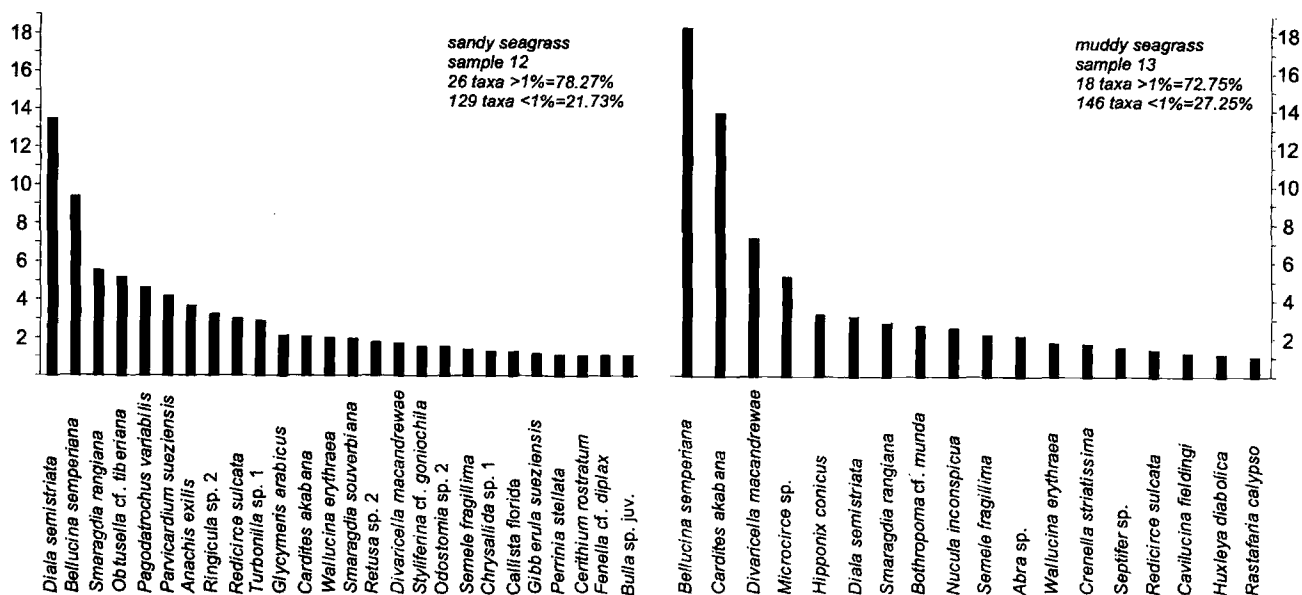Tab. 3. Number of taxa and diversity indices of samples.

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Fig. 5. Relative frequencies of taxa (complete data set) in samples from seagrass.

sandy seagrass (1) and muddy seagrass (1). A comparatively low number of species was found in samples from muddy sand (2), mud (2), and mangrove (1). The number of gastropod taxa is higher than that of bivalves in all samples, but is clearly dominant in samples from reef slopes, sand between coral patches, seagrass and the mangrove (tab. 3).

Using the transformed proportions of taxa in Table 3 as variables for a cluster analysis resulted also in a grouping according to sedimentary facies (fig. 9): at higher hierarchical levels two main clusters are obvious: samples from mud and muddy sand are lumped into one cluster characterized by low numbers of taxa, complete lack of polyplacophorans

and a comparatively weak dominance of gastropods; the second cluster, consisting of samples from seagrass, coral sand, reef slope and the mangrove channel is best characterized by a strong dominance of gastropod taxa; additional features are high numbers of taxa (except the mangrove) and the occurrence of polyplacophorans (except seagrass).

Individual numbers

Gastropods and bivalves are far more abundant in the 13 samples than are scaphopods and polyplacophorans.
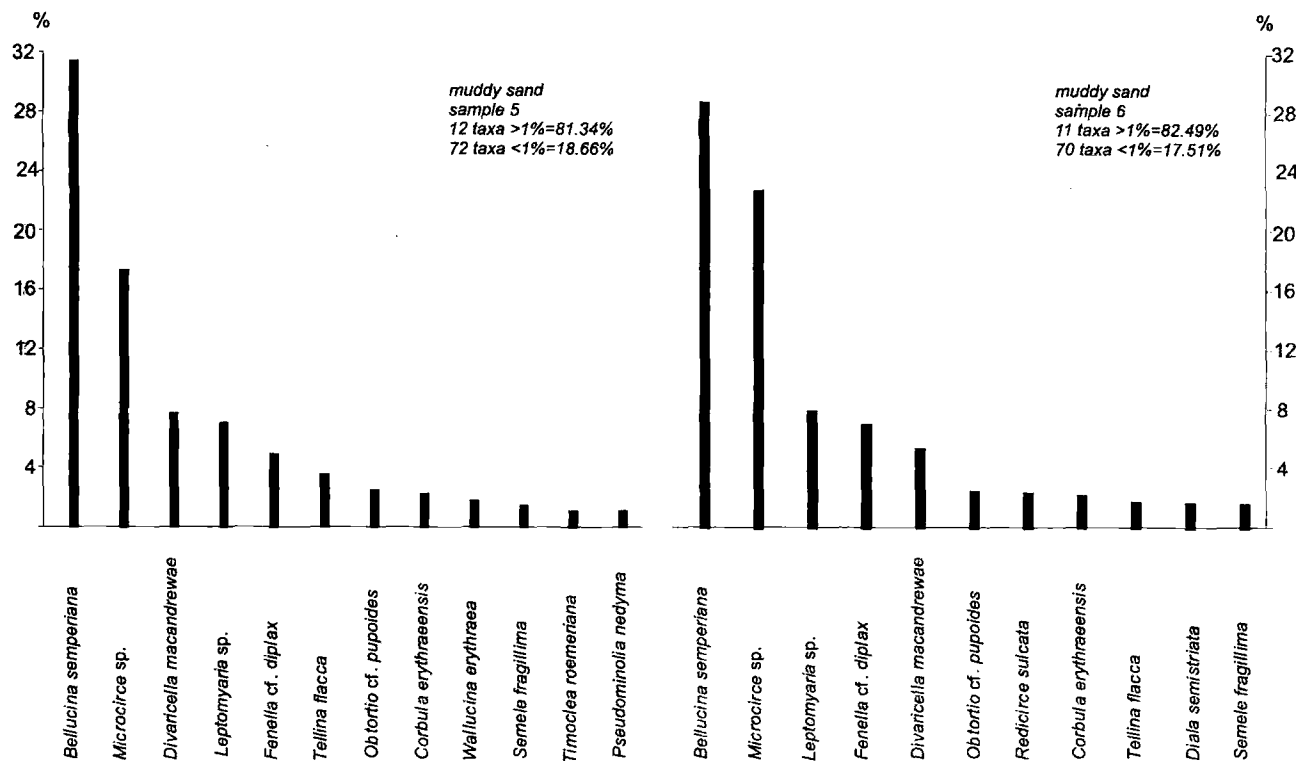


Fig. 6. Relative frequencies of taxa (complete data set) in samples from muddy sand.
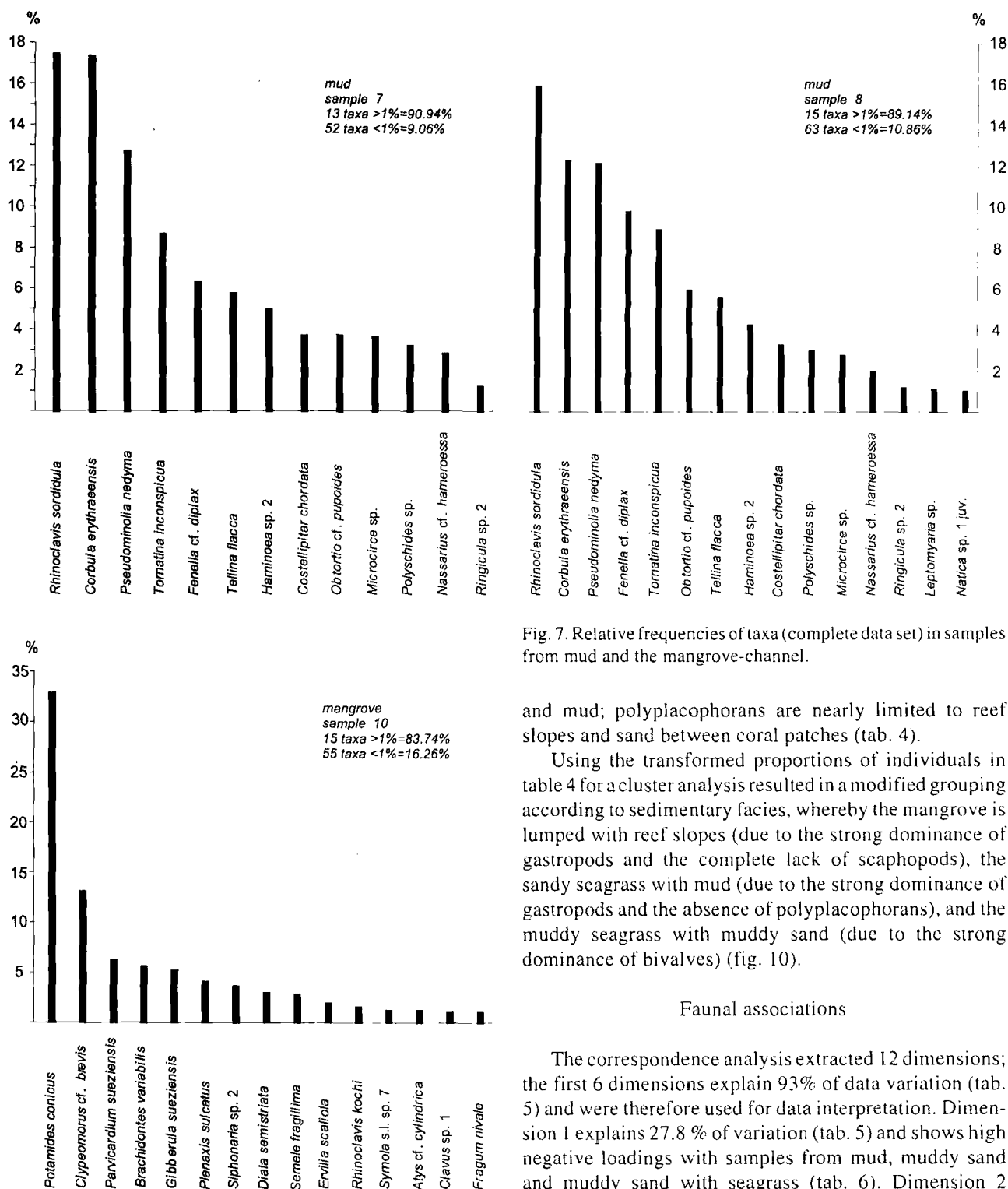
**%**

18
16
14
12
10
8
6
4
2

*mud
sample 7
13 taxa >1%=90.94%
52 taxa <1%=9.06%*

Rhinoclavis sordidula
Corbula erythraeensis
Pseudominolia nedyma
Tornatina inconspicua
Fenella cf. diplax
Tellina flacca
Haminoea sp. 2
Costellipitar chordata
Obtortio cf. pupoides
Microcirce sp.
Polyschides sp.
Nassarius cf. hameroessa
Ringicula sp. 2

**%**

18
16
14
12
10
8
6
4
2

*mud
sample 8
15 taxa >1%=89.14%
63 taxa <1%=10.86%*

Rhinoclavis sordidula
Corbula erythraeensis
Pseudominolia nedyma
Fenella cf. diplax
Tornatina inconspicua
Obtortio cf. pupoides
Tellina flacca
Haminoea sp. 2
Costellipitar chordata
Polyschides sp.
Microcirce sp.
Nassarius cf. hameroessa
Ringicula sp. 2
Leptomyaria sp.
Natica sp. 1 juv.

Fig. 7. Relative frequencies of taxa (complete data set) in samples from mud and the mangrove-channel.

**%**

35
30
25
20
15
10
5

*mangrove
sample 10
15 taxa >1%=83.74%
55 taxa <1%=16.26%*

Potamides conicus
Clypeomorus cf. brevis
Parvicardium sueziensis
Brachidontes variabilis
Gibberula sueziensis
Planaxis sulcatus
Siphonaria sp. 2
Diala semistriata
Semele fragillima
Ervilia scaliola
Rhinoclavis kochi
Symola s.l. sp. 7
Atys cf. cylindrica
Clavus sp. 1
Fragum nivale

Samples from the reef slope, mud, sandy seagrass and mangrove are clearly dominated by gastropods. In contrast, in samples from muddy sand and muddy seagrass, bivalves are the dominating faunal element. The four samples from sand between coral patches show a more balanced relation, with gastropods slightly dominating in samples 1 and 2 and bivalves slightly dominating in samples 3 and 4. Scaphopods and polyplacophorans are quantitatively rather unimportant and show strong facies restrictions. Scaphopods are mainly restricted to sand between coral patches

and mud; polyplacophorans are nearly limited to reef slopes and sand between coral patches (tab. 4).

Using the transformed proportions of individuals in table 4 for a cluster analysis resulted in a modified grouping according to sedimentary facies, whereby the mangrove is lumped with reef slopes (due to the strong dominance of gastropods and the complete lack of scaphopods), the sandy seagrass with mud (due to the strong dominance of gastropods and the absence of polyplacophorans), and the muddy seagrass with muddy sand (due to the strong dominance of bivalves) (fig. 10).

## Faunal associations

The correspondence analysis extracted 12 dimensions; the first 6 dimensions explain 93% of data variation (tab. 5) and were therefore used for data interpretation. Dimension 1 explains 27.8 % of variation (tab. 5) and shows high negative loadings with samples from mud, muddy sand and muddy sand with seagrass (tab. 6). Dimension 2 explains 19.2 % of variation (tab. 5) and shows high positive loadings with samples from mud (tab. 6). Dimension 3 explains 18.6 % of variation (tab. 5) and shows a high positive loading with the mangrove sample (tab. 6). Dimension 4 explains 15.5 % of variability (tab. 5) and shows high positive loadings with samples from muddy sand, reef slopes and mangrove (tab. 6). Dimension 5 explains 7 % of variation (tab. 5) and shows high negative loadings with the seagrass samples (tab. 6). Dimension 6 explains 4.8 % (tab. 5) of variation and shows a high negative loading with the sample from muddy seagrass

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Fig. 8. Cluster analyses dendrograms (Ward's method) based on absolute frequencies of taxa.



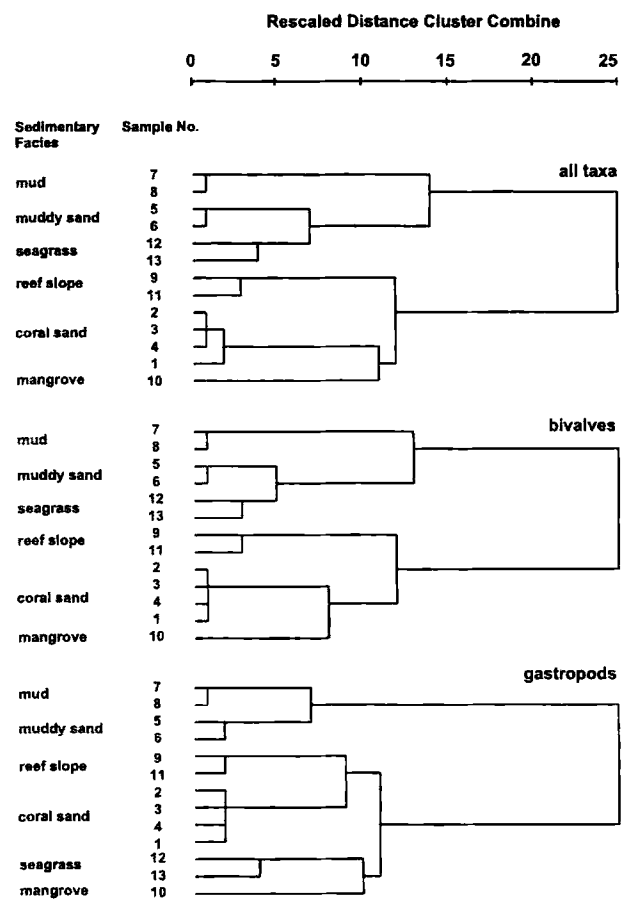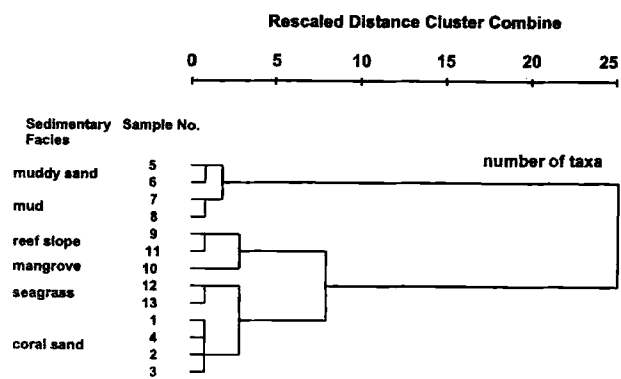Fig. 9. Cluster analyses dendrograms (Ward's method) based on numbers of taxa.
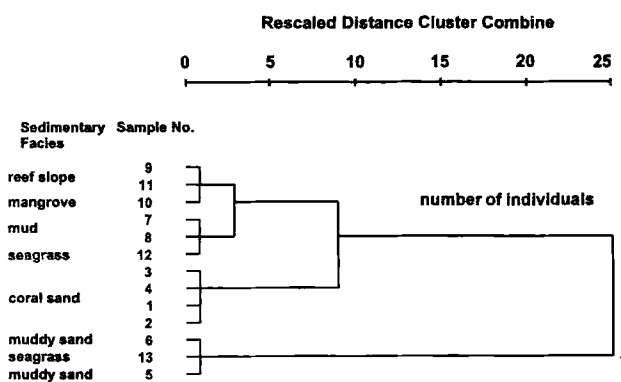


Fig. 10. Cluster analyses dendrograms (Ward's method) based on numbers of individuals.

and a significant positive loading with the sample from sandy seagrass (tab. 6). Samples from sand between coral patches are not explained explicitly by a single dimension, but show intermediate loadings with most dimensions (tab. 6).

The ordination of samples in the coordinate system of first two dimensions shows the distinct separation of classes, consistent with the cluster analyses (fig. 11). The diverse position of the seagrass communities, as demonstrated by the different cluster analysis, is caused by an intermediate position between muddy sand, mangrove, and sand between

coral patches. Additionally, the seagrass cluster does not show the same degree of homogeneity as other clusters, as indicated by the large distance between sandy seagrass and muddy seagrass (fig. 11 A).

The ordination of taxa shows two distinct groups (fig. 11): One closely coincides with the sample clusters (shaded areas in fig. 11 B, C), indicating a strong relationship between taxa and samples, the other, located between the sample clusters, demonstrates the degree of relationships to the cluster centroids (indicated by arrows in fig. 11 B, C).

| facies | sample no. | counted individuals no./sample | calculated individuals | | | | |
|---|---|---|---|---|---|---|---|
| | | | bivalves | gastropods | scaphopods | polyplacophorans | no./sample |
| sand between coral patches | 1 | 1880 | 32857 | 43781 | 1770 | 80 | 78488 |
| | 2 | 1694 | 40972 | 43918 | 2532 | 96 | 87518 |
| | 3 | 1464 | 39850 | 31268 | 1985 | 64 | 73167 |
| | 4 | 1488 | 34030 | 27531 | 2051 | 160 | 63772 |
| muddy sand | 5 | 740 | 11148 | 2607 | 64 | 0 | 13819 |
| | 6 | 898 | 14390 | 4155 | 2 | 0 | 18547 |
| mud | 7 | 2748 | 3796 | 6844 | 352 | 0 | 10992 |
| | 8 | 2412 | 2808 | 6532 | 308 | 0 | 9648 |
| reef slope | 9 | 1137 | 7876 | 24021 | 0 | 736 | 32633 |
| | 11 | 2766 | 21094 | 64832 | 0 | 2400 | 88326 |
| mangrove | 10 | 626 | 989 | 3666 | 0 | 24 | 4679 |
| seagrass | 11 | 3361 | 9238 | 18778 | 2 | 0 | 28018 |
| | 13 | 5168 | 8266 | 3046 | 6 | 0 | 11318 |
| | total no. | 26382 | 227314 | 280979 | 9072 | 3560 | 520925 |

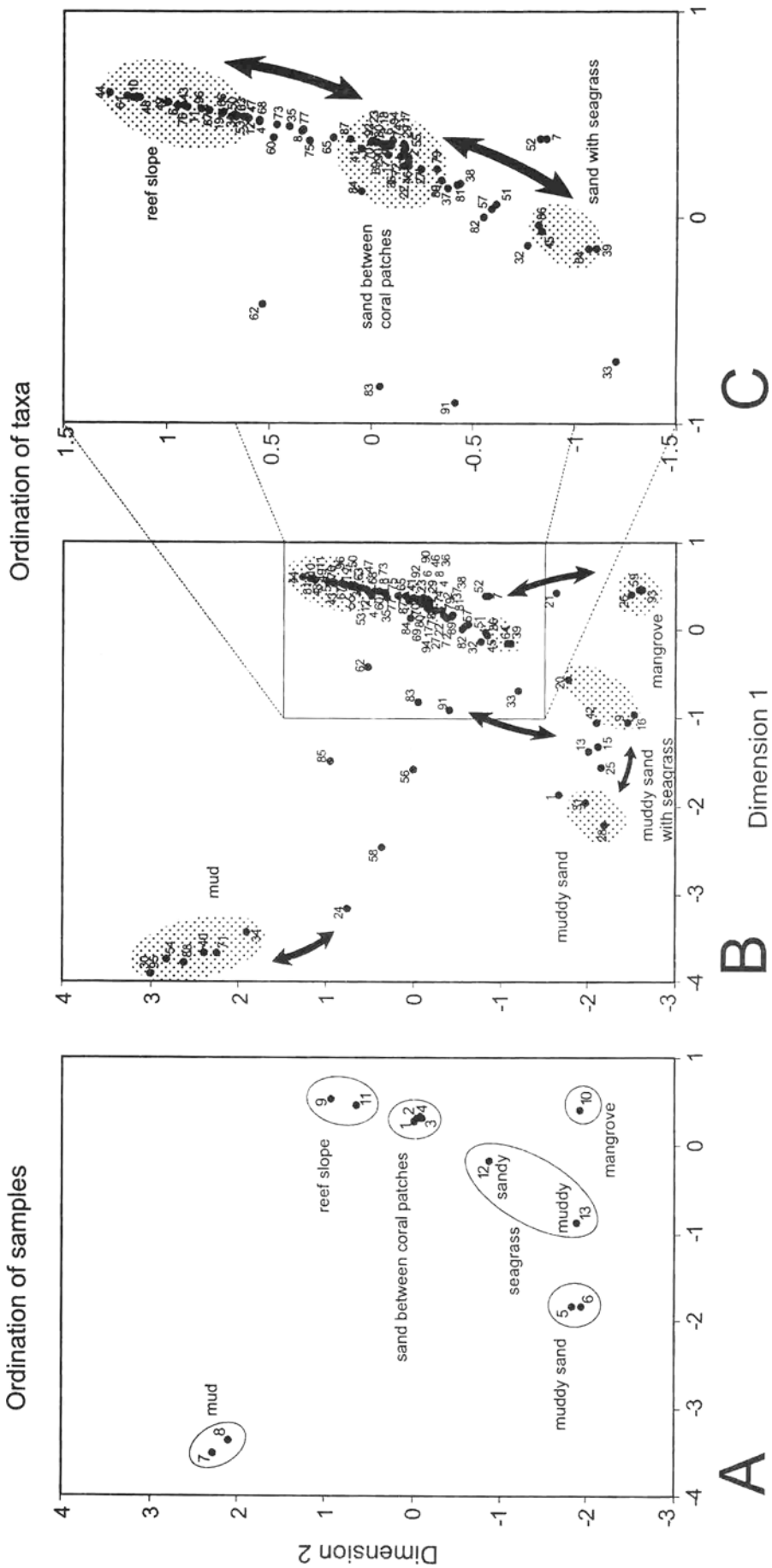Tab. 4. Counted and calculated individual numbers of samples.

Fig. 11. Ordination of samples (A) and taxa (B, C) using dimension 1 and dimension 2 of correspondence analysis. Numbers in fig. 11A are sample numbers and ellipses represent clusters gained by classification analysis (Wards method); numbers in fig. 11B and fig. 11C are numbers of taxa in tab. 7, tab. 8 and tab. 9.

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## Ordination of samples
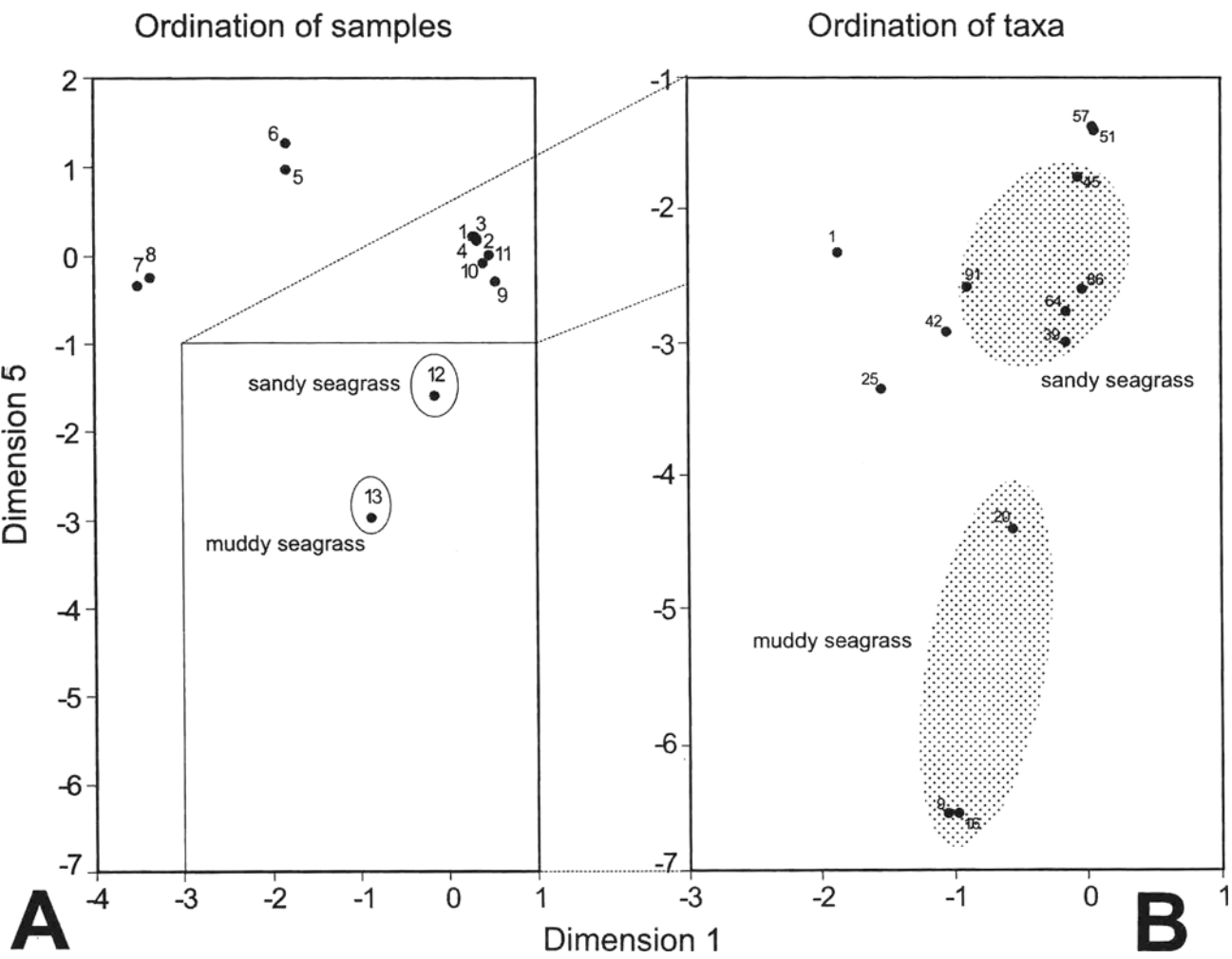
## Ordination of taxa



Fig.12. Ordination of samples (A) and taxa (B) using dimension 1 and dimension 5 of correspondence analysis. Numbers in fig. 12A are sample numbers and ellipses represent clusters gained by classification analysis (Wards method); numbers in fig. 11C are numbers of taxa in tab. 7, tab. 8 and tab. 9.

Based on factor loadings of taxa (tab. 7) and their positions relative to cluster centers (fig. 11, fig. 12), the taxa were grouped into associations (tab. 8). "Character-taxa" are restricted to a specific sedimentary facies, and

| Dimension | Proportion Explained | Cumulative Proportion |
|---|---|---|
| 1 | 0.278 | 0.278 |
| 2 | 0.192 | 0.470 |
| 3 | 0.186 | 0.656 |
| 4 | 0.155 | 0.811 |
| 5 | 0.070 | 0.882 |
| 6 | 0.048 | 0.930 |
| 7 | 0.041 | 0.971 |
| 8 | 0.014 | 0.985 |
| 9 | 0.006 | 0.991 |
| 10 | 0.004 | 0.995 |
| 11 | 0.003 | 0.998 |
| 12 | 0.002 | 1.000 |
| Total | 1.000 | |

Tab. 5. Proportions explained by the 12 dimensions of correspondence analysis.

are therefore characteristic for a specific environment (WESTHOFF & VAN DER MAAREL, 1973). "Intermediate taxa", in contrast, indicate transitions between different sedimentary facies (tab. 8). A small number of "totally intermediate taxa" are not related to specific sedimentary environments, but shows a very indistinct and broad distribution (*Timoclea roemeriana, Fenella* cf. *diplax, Obtortio* cf. *pupoides, Natica* sp. 1 juv., *Atys* cf. *cylindrica, Haminoea* sp. 2).

The mud facies is very distinct and best characterized by the bivalves *Costellipitar chordatum* and *Corbula erythraeensis*, the gastropods *Pseudominolia nedyma, Rhinoclavis sordidula, Nassarius* cf. *hameroessa* and *Tornatina inconspicua*, and the scaphopod *Polyschides* sp. This association is termed the "*Rhinoclavis sordidula - Corbula erythraeensis - Pseudominolia nedyma* association" (Pl. 56/1, 2, 3, 10) after its three most abundant constituents (tab. 9) and shows only minor transitions to the fauna of muddy sands, indicated by the bivalve *Tellina flacca*. The characteristic taxa of this facies are also the prevalent taxa because they are quantitatively dominant (tab. 9).

The fauna of muddy sands is best characterized by the bivalves *Leptomyaria* sp. and *Microcirce* sp.; strong transitions are evident to the muddy seagrass fauna as indicated by some bivalves (*Nucula inconspicua, Bellucina*

Fig. 13. Dendrograms of cluster analyses (Ward's method) on diversity indices.



Fig. 14. Cluster analysis (Ward's method) on bivalve feeding strategies and substrate relations.

*semperiana, Divaricella macandrewae, Abra* sp.) and only one gastropod (*Bothropoma* cf. *munda*). This association is termed the "*Microcirce* sp. - *Leptomyaria sp.* association" (Pl. 56/4, 5, 6, 9), after its characteristic constituents, but is quantitatively dominated by *Bellucina semperiana* (tab. 9).

The seagrass fauna is characterized by the bivalves *Crenella striatissima, Rastafaria calypso*, and *Cardites akabana*, which typically occur in muddy seagrass, and the gastropods *Perrinia stellata, Smaragdia* spp., *Anachis exilis, Bulla* sp. juv., and *Ringicula* sp. 2, which typically occur in sandy seagrass. Considering the most abundant characteristic representatives, the association in sandy seagrass is termed the "*Smaragdia* spp. - *Perrinia stellata - Anachis exilis* - association" (Pl. 57/4, 7, 10), which is quantitatively dominated by *Diala* spp., *Bellucina semperiana* and *Smaragdia* spp. (tab. 9). This association in muddy seagrass is termed the "*Crenella striatissima - Rastafaria calypso - Cardites akabana* association" (Pl. 56/7, 8, 11, 12; Pl. 57/1, 2), which is quantitatively dominated by *Bellucina semperiana* and *Cardites akabana* (tab. 9). A broad transition from sandy seagrass to the "sand between coral patches association" is indicated by various gastropods (*Obtusella* cf. *tiberiana, Pagodatrochus variabilis, Cerithium rostratum, Styliferina* cf. *goniochila, Syrnola* s.l. spp. and *Turbonilla* spp.) and the bivalve *Redicirce sulcata*.

The fauna in sand between coral patches is characterized by an enormous number of bivalves (*Huxleya diabolica*, Glycymerididae, *Pillucina fischeriana, Wallucina erythraea, Parvicardium sueziensis, Semele fragillima, Callista florida*)
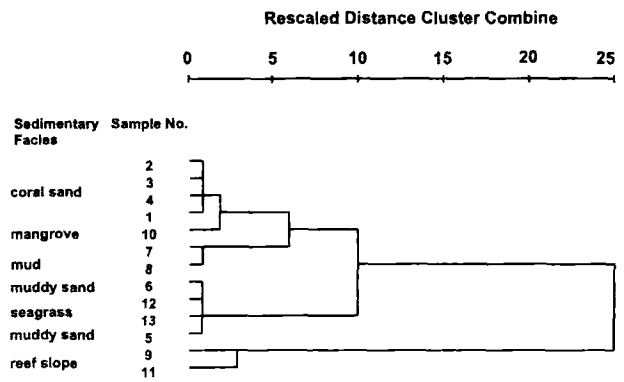
and gastropods (*Phasianella* spp., Trochidae gen. et sp. indet. 1, *Peasiella* spp., *Diala* spp., *Euplica ionida, Gibberula* spp., *Nassarius* cf. *delicatus, Ancilla* sp., *Clavus* spp., *Odostomia* spp., *Pyramidella* spp., *Haminoea* sp. 1, *Mamilloretusa* ? sp., *Retusa* sp. 3., *Ringicula* sp. 1, *Tornatina* sp. 1-3.) and the scaphopod *Gadila* sp. The association is termed the "*Glycymeris* spp. - *Parvicardium sueziensis - Diala* spp. association" (Pl. 57/5, 6, 8, 9, 11) after its most abundant characteristic representatives, which are also the prevalent taxa (tab. 9).

The bivalves *Barbatia* spp., *Septifer* sp. and the gastropods *Patelloida* spp., *Hipponix conicus, Coralliophila* spp., Cerithiopsidae and Eulimidae show strong transitions from sand between coral patches to the reef slope. The bivalves *Brachidontes variabilis, Fragum nivale* and the gastropod *Clypeomorus* cf. *brevis* show a weak transition to the mangrove.

The reef slope fauna is best characterized by the bivalves *Acar plicata, Limopsis sp.*, Spondylidae, Anomioidea, Ostreoidea, Chamoidea, the gastropods *Collonista arsinoensis, Pisulina adamsiana, Rissoina* spp., *Stosicia* sp., *Cerithium zebrum, Cerithium egenum, Plesiotrochus souverbianus, Hipponix* sp. 2, Buccinidae gen. et sp. indet. 1, *Zafra* cf. *selasphora, Zafrona isomella*, and Triphoridae and Polyplacophora. The association on reef slopes is termed the "*Rissoina* spp. - Triphoridae - Ostreoidea association" (Pl. 57/13-15) according to the three most abundant characteristic representatives, which are also the prevalent taxa (tab. 9).

The "mangrove association" is best characterized by

| sample no. | bottom facies | Dim 1 | Dim 2 | Dim 3 | Dim 4 | Dim 5 | Dim 6 |
|---|---|---|---|---|---|---|---|
| 1 | sand between coral patches | 0.293 | -0.012 | -0.073 | -0.451 | 0.203 | -0.094 |
| 2 | sand between coral patches | 0.330 | -0.055 | -0.008 | -0.519 | 0.158 | -0.027 |
| 3 | sand between coral patches | 0.322 | -0.102 | -0.055 | -0.685 | 0.201 | -0.168 |
| 4 | sand between coral patches | 0.343 | -0.084 | -0.028 | -0.568 | 0.186 | -0.149 |
| 5 | muddy sand | -1.817 | -1.827 | 0.67 | 0.983 | 0.962 | 0.105 |
| 6 | muddy sand | -1.828 | -1.940 | 0.722 | 1.070 | 1.273 | 0.304 |
| 7 | mud | -3.509 | 2.281 | -0.732 | -0.629 | -0.345 | -0.098 |
| 8 | mud | -3.364 | 2.098 | -0.671 | -0.571 | -0.239 | -0.018 |
| 9 | reef slope | 0.538 | 0.940 | 0.338 | 1.674 | -0.299 | 0.590 |
| 10 | mangrove | 0.414 | -1.914 | -8.359 | 2.049 | -0.080 | 0.016 |
| 11 | reef slope | 0.474 | 0.648 | 0.228 | 0.962 | 0.014 | -0.210 |
| 12 | sand with seagrass | -0.155 | -0.867 | 0.184 | -0.473 | -1.588 | 1.793 |
| 13 | muddy sand with seagrass | -0.871 | -1.884 | 0.672 | 0.617 | -2.970 | -2.630 |

Tab. 6. Loadings of samples by dimensions 1-6.

| no. | taxa | Dim 1 | Dim 2 | Dim 3 | Dim 4 | Dim 5 | Dim 6 |
|---|---|---|---|---|---|---|---|
| 1 | Nucula inconspicua | -1.861 | -1.659 | 0.631 | 0.862 | -2.313 | -3.176 |
| 2 | Huxleya diabolica | 0.302 | -0.17 | 0.026 | -0.642 | 0.041 | -0.29 |
| 3 | Acar plicata | 0.498 | 0.692 | 0.232 | 1.039 | -0.047 | 0.176 |
| 4 | Barbatia spp. | 0.47 | 0.548 | 0.179 | 0.701 | 0.023 | 0.165 |
| 5 | Limopsis sp. | 0.549 | 0.948 | 0.34 | 1.632 | -0.081 | -0.224 |
| 6 | Glycymeris spp. | 0.355 | -0.092 | -0.046 | -0.793 | 0.323 | -0.19 |
| 7 | Brachidontes variabilis | 0.387 | -0.858 | -3.808 | 0.544 | 0.193 | -0.175 |
| 8 | Septifer sp. | 0.424 | 0.341 | 0.142 | 0.328 | 0.007 | -0.123 |
| 9 | Crenella striatissima | -1.045 | -2.460 | 0.893 | 0.899 | -6.567 | -7.027 |
| 10 | Spondylidae | 0.588 | 1.163 | 0.421 | 2.235 | -0.55 | 1.330 |
| 11 | Anomioidea | 0.539 | 0.904 | 0.324 | 1.567 | -0.184 | 0.258 |
| 12 | Ostreoidea | 0.493 | 0.629 | 0.22 | 0.873 | 0.048 | -0.142 |
| 13 | Bellucina semperiana | -1.369 | -2.007 | 0.709 | 0.836 | 0.121 | 0.184 |
| 14 | Cavilucina fieldingi | 0.306 | -0.157 | 0.032 | -0.578 | -0.015 | -0.685 |
| 15 | Divaricella macandrewae | -1.327 | -2.107 | 0.722 | 0.869 | -0.526 | -0.708 |
| 16 | Rastafaria sp. | -0.964 | -2.528 | 0.913 | 0.903 | -6.569 | -7.055 |
| 17 | Pillucina fischeriana | 0.354 | -0.082 | -0.032 | -0.747 | 0.323 | -0.201 |
| 18 | Wallucina erythraea | 0.312 | -0.079 | 0.025 | -0.518 | 0.21 | -0.229 |
| 19 | Chamoidea gen. et sp. indet | 0.515 | 0.731 | 0.26 | 1.139 | -0.113 | 0.299 |
| 20 | Cardites akabana | -0.555 | -1.763 | 0.589 | 0.243 | -4.402 | -3.140 |
| 21 | Fragum nivale | 0.428 | -1.623 | -6.980 | 1.449 | 0.072 | -0.157 |
| 22 | Parvicardium sueziensis | 0.339 | -0.164 | -0.171 | -0.774 | 0.213 | -0.047 |
| 23 | Tellina lactea | 0.368 | -0.03 | -0.014 | -0.645 | 0.332 | -0.334 |
| 24 | Tellina flacca | -3.163 | 0.764 | -0.198 | 0.075 | 0.583 | 0.101 |
| 25 | Abra sp. | -1.546 | -2.153 | 0.796 | 0.99 | -3.341 | -4.215 |
| 26 | Ervilia scaliola | 0.415 | -2.493 | -10.596 | 2.789 | -0.464 | 0.449 |
| 27 | Semele fragilima | 0.24 | -0.241 | -0.146 | -0.574 | 0.041 | -0.238 |
| 28 | Leptomyaria sp. | -2.196 | -2.191 | 0.834 | 1.394 | 2.358 | 0.559 |
| 29 | Callista florida | 0.334 | -0.157 | -0.051 | -0.879 | 0.268 | -0.124 |
| 30 | Costellipitar sp. | -3.906 | 3.003 | -0.977 | -0.916 | -0.872 | -0.171 |
| 31 | Microcirce sp. | -1.957 | -1.972 | 0.75 | 1.172 | 1.492 | 0.036 |
| 32 | Redicirce sulcata | -0.131 | -0.768 | 0.191 | -0.41 | -0.491 | 0.727 |
| 33 | Timoclea roemeriana | -0.693 | -1.203 | 0.428 | 0.281 | 0.83 | 0.159 |
| 34 | Corbula erythraeensis | -3.439 | 1.916 | -0.578 | -0.374 | -0.199 | -0.1 |
| 35 | Patelloida spp. | 0.447 | 0.404 | 0.075 | 0.43 | 0.132 | -0.06 |
| 36 | Phasianella spp. | 0.274 | -0.181 | -0.031 | -0.715 | 0.132 | -0.223 |
| 37 | Obtusella cf. tiberiana | 0.145 | -0.373 | -0.014 | -0.677 | -0.547 | 1.045 |
| 38 | Pagodatrochus variabilis | 0.172 | -0.434 | 0.018 | -0.724 | -0.612 | 0.907 |
| 39 | Perrinia stellata | -0.146 | -1.106 | 0.276 | -0.518 | -2.990 | 1.784 |
| 40 | Pseudominolia nedyma | -3.661 | 2.389 | -0.757 | -0.628 | -0.323 | -0.093 |
| 41 | Trochidae gen. et sp. indet 1 | 0.341 | 0.052 | -0.046 | -0.55 | 0.39 | -0.254 |
| 42 | Bothropoma cf. munda | -1.053 | -2.102 | 0.783 | 0.865 | -2.917 | -2.791 |
| 43 | Collonista arsinoensis | 0.545 | 0.921 | 0.332 | 1.580 | -0.105 | -0.086 |
| 44 | Pisulina adamsiana | 0.61 | 1.283 | 0.468 | 2.540 | -0.673 | 1.608 |
| 45 | Smaragdia spp. | -0.061 | -0.834 | 0.116 | -0.496 | -1.750 | 1.570 |
| 46 | Peasiella spp | 0.361 | -0.159 | -0.448 | -0.699 | 0.413 | -0.297 |
| 47 | Rissoina spp. | 0.485 | 0.605 | 0.206 | 0.815 | 0.077 | -0.195 |
| 48 | Stosicia sp. | 0.583 | 1.136 | 0.412 | 2.142 | -0.413 | 0.805 |
| 49 | Bittium cf. zebrum | 0.56 | 0.998 | 0.362 | 1.828 | -0.423 | 1.106 |
| 50 | Cerithium egenum | 0.501 | 0.671 | 0.237 | 0.98 | 0.031 | -0.152 |
| 51 | Cerithium rostratum | 0.073 | -0.614 | 0.118 | -0.574 | -1.396 | 0.554 |
| 52 | Clypeomorus cf. brevis | 0.387 | -0.825 | -3.520 | 0.374 | 0.255 | -0.2 |
| 53 | Plesiotrochus souverbianus | 0.5 | 0.668 | 0.24 | 1.002 | -0.084 | 0.322 |
| 54 | Rhinoclavis sordidula | -3.729 | 2.820 | -0.917 | -0.879 | -0.597 | -0.16 |
| 55 | Diala spp. | 0.254 | -0.18 | 0.019 | -0.356 | -0.351 | 0.464 |
| 56 | Fenella cf. diplax | -1.580 | 0.004 | 0.085 | 0.24 | 0.611 | 0.273 |
| 57 | Styliferina cf. goniochila | 0.047 | -0.587 | 0.149 | -0.518 | -1.363 | 2.106 |
| 58 | Obtortio cf. pupoides | -2.450 | 0.357 | -0.082 | 0.025 | 0.465 | 0.387 |
| 59 | Potamides conicus | 0.467 | -2.585 | -11.464 | 3.068 | -0.174 | 0.042 |
| 60 | Hipponix conicus | 0.396 | 0.483 | 0.308 | 1.110 | -0.566 | -0.373 |
| 61 | Hipponix sp. 2 | 0.593 | 1.193 | 0.434 | 2.296 | -0.514 | 1.116 |
| 62 | Natica sp. 1 juv. | -0.417 | 0.532 | -0.469 | -0.101 | 0.18 | -0.244 |
| 63 | Buccinidae gen. et sp. indet. 1 | 0.497 | 0.868 | 0.228 | 0.973 | -0.006 | 0.001 |
| 64 | Anachis axillis | -0.148 | -1.062 | 0.249 | -0.6 | -2.766 | 3.044 |
| 65 | Euplica Ionida | 0.393 | 0.192 | 0.064 | -0.069 | 0.125 | -0.026 |
| 66 | Zafra cf. selasphora | 0.512 | 0.731 | 0.264 | 1.121 | -0.007 | -0.121 |
| 67 | Zafrona isomella | 0.524 | 0.8 | 0.287 | 1.320 | -0.159 | 0.394 |
| 68 | Coralliophila spp. | 0.475 | 0.547 | 0.182 | 0.69 | 0.079 | -0.085 |
| 69 | Gibberula spp. | 0.36 | -0.053 | -0.501 | 0.008 | -0.087 | -0.01 |
| 70 | Nassarius cf. delicatus | 0.369 | 0.002 | -0.014 | -0.584 | 0.317 | -0.223 |
| 71 | Nassarius cf. hameroessa | -3.660 | 2.248 | -0.714 | -0.581 | -0.253 | -0.088 |
| 72 | Ancilla sp. | 0.305 | -0.142 | -0.007 | -0.739 | 0.167 | -0.149 |
| 73 | Cerltolurris sp. | 0.454 | 0.462 | 0.159 | 0.505 | 0.149 | -0.418 |
| 74 | Clavus spp. | 0.378 | -0.101 | -0.579 | -0.39 | 0.295 | -0.203 |
| 75 | Cerithiopsidae | 0.382 | 0.307 | 0.178 | 0.419 | -0.094 | 0.176 |
| 76 | Triphoridae | 0.545 | 0.921 | 0.331 | 1.606 | -0.216 | 0.394 |
| 77 | Eulimidae | 0.43 | 0.334 | 0.142 | 0.278 | 0.035 | -0.103 |
| 78 | Chrysallida spp. | 0.255 | -0.157 | 0.008 | -0.642 | -0.068 | 0.244 |
| 79 | Odostomia spp. | 0.239 | -0.316 | 0.012 | -0.696 | -0.512 | 0.533 |
| 80 | Pyramidella spp | 0.348 | -0.068 | -0.115 | -0.713 | 0.346 | -0.222 |
| 81 | Symola s.l. spp | 0.164 | -0.421 | -0.367 | -0.395 | 0.033 | 0.082 |
| 82 | Turbonilla spp. | 0.007 | -0.552 | 0.097 | -0.554 | -0.782 | 1.302 |
| 83 | Atys cf. cylindrica | -0.816 | -0.044 | -0.943 | -0.091 | 0.414 | -0.115 |
| 84 | Haminoea sp. 1 | 0.134 | 0.051 | -0.104 | -0.791 | 0.256 | -0.336 |
| 85 | Haminoea sp. 2 | -1.486 | 0.962 | -0.309 | -0.495 | 0.149 | -0.193 |
| 86 | Bulla sp. juv. | -0.027 | -0.816 | 0.227 | -0.468 | -2.590 | 3.040 |
| 87 | Mamilloretusa ? sp. | 0.389 | 0.104 | 0.027 | -0.358 | 0.345 | -0.346 |
| 88 | Tomatina inconspicua | -3.778 | 2.626 | -0.846 | -0.749 | -0.453 | -0.115 |
| 89 | Retusa sp. 2 | 0.187 | -0.342 | -0.027 | -0.642 | -0.092 | 0.43 |
| 90 | Ringicula sp. 1 | 0.359 | -0.075 | -0.054 | -0.796 | 0.386 | -0.254 |
| 91 | Ringicula sp. 2 | -0.898 | -0.411 | 0.046 | -0.615 | -2.580 | 2.907 |
| 92 | Tomatina sp.1-3 | 0.38 | -0.001 | -0.031 | -0.611 | 0.351 | -0.266 |
| 93 | Siphonaria sp. 2 | 0.469 | -2.612 | -11.582 | 3.108 | -0.181 | 0.045 |
| 94 | Gadila sp. | 0.359 | -0.097 | -0.049 | -0.844 | 0.421 | -0.285 |
| 95 | Polyschides sp. | -3.903 | 3.000 | -0.976 | -0.915 | -0.669 | -0.168 |
| 96 | Polyplacophora | 0.533 | 0.833 | 0.226 | 1.436 | -0.072 | -0.088 |

Tab. 7. Loadings of taxa (reduced data set) by dimensions 1-6.

the gastropods *Potamides conicus* and *Siphonaria* sp. 2 and is termed the "*Potamides conicus* and *Siphonaria* sp. 2 - association" (Pl. 57/ 3, 12) after these two most abundant character-taxa. Quantitatively this association is dominated by the prevalent taxa *Potamides conicus* and *Clypeomorus* cf. *brevis*.

## Diversity

Diversity is highest in samples from sand between coral patches, which have highest Simpson and Information indices and highest Evenness Index; reef slope samples have a diversity that is almost as high (with one sample having the highest Information index), followed by seagrass samples, which have distinctly lower information indices and lower evenness. Samples from muddy sand, mud and the mangrove have similar and comparatively low diversity values (tab. 3).

Cluster analyses based on diversity indices alone also revealed a slightly modified and simplified relation to sedimentary facies. Two main clusters are obvious. The first which is characterized by high diversity values consists of samples from reef slopes, sand between coral patches and seagrass. The second, characterized by low diversity indices consists of the samples from muddy sand, mud and the mangrove (Fig. 13).

## Feeding strategies and substrate relations of bivalves

Generalized feeding strategies (for lucinids after LE PENNEC et al., 1995; for all other families after MORTON, 1983), relations to substrate (using information given in OLIVER, 1992), and relationships to sedimentary facies are provided for the bivalve taxa (tab. 10, tab. 11). Among the feeding strategies, we differentiated chemosymbionts, suspension feeders, and deposit feeders, and among substrate relations, we differentiated burrowing, byssally attached, and cemented bivalves. In terms of relative abundances, associations in sand between coral patches are slightly, and muds are clearly dominated by burrowing suspension feeders. In muddy sand and seagrass areas, burrowing chemosymbionts are very abundant. Reef slopes have very high abundances of byssally attached and cemented suspension feeders. The mangrove shows similar abundances of burrowing deposit feeders and suspension feeders and byssally attached suspension feeders (tab. 11).

Cluster analysis based on feeding strategies and substrate relations yields a slightly simplified grouping according to sedimentary facies; note that muddy sands are lumped with seagrass. At higher hierarchical levels, two major groups are recognized, one dominated by epifaunal bivalves (reef slopes) and the other by infaunal bivalves (all other sedimentary facies) (fig. 14).

Factor analysis on bivalve taxa extracted four dominating factors (tab. 12, tab. 13), which explain the distribution of bivalves and largely coincide with the results of the cluster analysis: factor one explains the distribution of bivalves in sand between coral patches, factor 2 the distribution in muddy sand and seagrass, factor three in mud and factor 4 on reef slopes. The mangrove sample is not explained explicitly, but shows similar loading-variations as samples from sand between coral patches.

A factor analysis on gastropod taxa also extracted four relevant factors (tab. 14, tab. 15), which explain their distribution: factor 1 explains the co-occurrence of gastropods in sand between coral patches and seagrass, factor 2 the co-

occurrence in sand between coral patches and reef slopes, factor 3 the distribution of gastropods in muddy sand and factor 4 the distribution of gastropods in mud.

## Fragmentation

Fragments are far more numerous than whole individuals, contributing more than 88% to the total mollusc remains of the investigated samples (tab. 16). Nevertheless differences in the sedimentary facies are evident: the number of fragments is highest in samples from sand between coral patches, sandy seagrass and the *Porites* dominated reef slope, and lowest in samples from mud and the mangrove; it is intermediate in samples from muddy sand, muddy sand with seagrass and the *Acropora - Millepora* dominated reef slope (tab. 16). The proportion of fragments is lowest in samples from mud and the mangrove and highest in samples from muddy sand and sandy seagrass. This ratio is rather intermediate in samples from sand between coral patches, the reef slope and muddy sand with seagrass (tab. 16).

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**Tab. 8. — Taxa assemblages (Character-taxa) by habitat**

**reef slope — Character-taxa**
- 3 *Acar plicata*
- 5 *Limopsis* sp.
- 10 *Spondylidae*
- 11 *Anomioidea*
- 12 **Ostreoidea**
- 19 **Chamoidea**
- 43 *Collonista arsinoensis*
- 44 *Pisulina adamsiana*
- 47 **Rissoina spp.**
- 48 *Stosicia* sp.
- 49 *Cerithium zebrum*
- 50 *Cerithium egenum*
- 53 *Plesiotrochus souverbianus*
- 61 *Hipponix* sp. 2
- 63 Buccinidae gen. et sp. indet. 1
- 66 *Zafra* cf. *selasphora*
- 67 *Zafrona isomella*
- 76 **Triphoridae**
- 96 *Polyplacophora*
- Intermediate taxa transition to sand between coral patches
- 4 *Barbatia* spp.
- 8 *Septifer* sp.
- 35 *Patelloida* spp.
- 60 *Hipponix conicus*
- 68 *Coralliophila* spp.
- 73 *Ceritoturris* sp.
- 75 *Cerithiopsidae*
- 77 *Eulimidae*

**sand between coral patches — Character-taxa**
- 2 *Huxleya diabolica*
- 6 **Glycymeris spp.**
- 17 *Pillucina fischeriana*
- 18 *Wallucina erythraea*
- 22 **Parvicardium sueziensis**
- 27 *Semele fragillima*
- 29 *Callista florida*
- 36 (*Phasianella* spp.)
- 41 Trochidae gen. et sp. indet. 1
- 46 *Peasiella* spp
- 55 **Diala spp.**
- 65 *Euplica ionida*
- 69 *Gibberula* spp.
- 70 *Nassarius* cf. *delicatus*
- 72 *Ancilla* sp.
- 74 *Clavus* spp.
- 79 *Odostomia* spp.
- 80 *Pyramidella* spp.
- 84 *Haminoea* sp. 1
- 87 *Mamilloretusa* ? sp
- 89 *Retusa* sp. 2
- 90 *Ringicula* sp. 1
- 92 *Tornatina* sp1-3
- 94 *Gadila* sp.
- Intermediate taxa (1) transition to reef slope
- 4 *Barbatia* spp.
- 8 *Septifer* sp.
- 35 *Patelloida* spp.
- 60 *Hipponix conicus*
- 68 *Coralliophila* spp.
- 73 *Ceritoturris* sp.
- 75 *Cerithiopsidae*
- 77 *Eulimidae*
- Intermediate taxa (2) transition to sandy seagrass
- 32 *Redicirce sulcata*
- 37 *Obtusella* cf. *tiberiana*
- 38 *Pagodatrochus variabilis*
- 51 *Cerithium rostratum*
- 57 *Styliferina* cf. *goniochila*
- 81 *Syrnola* s.l. spp.
- 82 *Turbonilla* spp.
- Intermediate taxa (3) transition to mangrove
- 7 *Brachidontes variabilis*
- 21 *Fragum nivale*
- 52 *Clypeomorus* cf. *brevis*

**seagrass — Character-taxa**
- 9 *Crenella striatissima* (m)
- 16 *Rastafaria calypso* (m)
- 20 *Cardites akabana* (m)
- 39 *Perrinia stellata* (s)
- 45 *Smaragdia* spp. (s)
- 64 *Anachis exilis* (s)
- 86 *Bulla* sp. juv (s)
- 91 *Ringicula* sp. 2 (s)
- Intermediate taxa (1) transition to muddy sand
- 1 *Nucula inconspicua*
- 13 *Bellucina semperiana*
- 15 *Divaricella macandrewae*
- 25 *Abra* sp.
- 42 (*Bothropoma* cf. *munda*)
- Intermediate taxa (2) transition to sand between coral patches
- 32 *Redicirce sulcata*
- 37 *Obtusella* cf. *tiberiana*
- 38 *Pagodatrochus variabilis*
- 51 (*Cerithium rostratum*)
- 57 *Styliferina* cf. *goniochila*
- 81 *Syrnola* s.l. spp.
- 82 *Turbonilla* spp.

**mangrove — Character-taxa**
- 26 (*Ervilia scaliola*)
- 59 *Potamides conicus*
- 93 *Siphonaria* sp. 2
- Intermediate taxa transition to sand between coral patches
- 7 *Brachidontes variabilis*
- 21 (*Fragum nivale*)
- 52 *Clypeomorus* cf. *brevis*

**mud — Character-taxa**
- 30 *Costellipitar chordata*
- 34 *Corbula erythraeensis*
- 40 *Pseudominolia nedyma*
- 54 *Rhinoclavis sordidula*
- 71 *Nassarius* cf. *hameroessa*
- 88 *Tomatina inconspicua*
- 95 *Polyschides* sp.
- Intermediate taxa transition to muddy sand
- 24 *Tellina flacca*

**muddy sand — Character-taxa**
- 28 *Leptomyaria* sp.
- 31 *Microcirce* sp.
- Intermediate taxa (1) transition to muddy seagrass
- 1 *Nucula inconspicua*
- 13 *Bellucina semperiana*
- 15 *Divaricella macandrewae*
- 25 *Abra* sp.
- 42 (*Bothropoma* cf. *munda*)
- Intermediate taxa (2) transition to mud
- 24 *Tellina flacca*

Tab. 8. Taxa assemblages according to their factor loadings and positions to cluster centres. For special status of *Cerithium rostratum*, *Bothropoma* cf. *munda*, *Phasianella* spp., *Ervilia scaliola* and *Fragum nivale* refer to the discussion in the text. (m) = character taxa for muddy seagrass, (s) = character taxa for sandy seagrass. Bold taxa define assemblages.

| number | taxa | sand between coral patches | | | | reef slope | | seagrass | | mangrove | muddy sand | | mud | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 9 | 11 | 12 | 13 | 10 | 5 | 6 | 7 | 8 |
| 1 | Nucula inconspicua | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.08 | 0.00 | 0.89 | 0.67 | 0.45 | 0.58 |
| 2 | Huxleya diabolica | 0.62 | 2.07 | 1.52 | 1.70 | 0.00 | 0.35 | 0.66 | 1.38 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 |
| 3 | Acar plicata | 0.67 | 0.18 | 0.42 | 0.06 | 2.77 | 1.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | Barbatia spp. | 1.18 | 0.71 | 0.31 | 0.24 | 3.21 | 1.26 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 5 | Limopsis sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.91 | 1.82 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 6 | Glycymeris spp. | 11.72 | 10.42 | 11.77 | 11.75 | 0.00 | 0.74 | 2.59 | 0.19 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | Brachidontes variabilis | 0.12 | 0.27 | 0.16 | 0.24 | 0.00 | 0.04 | 0.00 | 0.00 | 6.44 | 0.00 | 0.00 | 0.04 | 0.00 |
| 8 | Septifer sp. | 2.56 | 2.47 | 2.51 | 2.85 | 6.35 | 4.34 | 0.47 | 1.81 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | Crenella striatissima | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 |
| 10 | Spondylidae | 0.05 | 0.04 | 0.05 | 0.00 | 4.35 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 11 | Anomioidea | 0.07 | 0.05 | 0.00 | 0.06 | 1.15 | 0.61 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 12 | Ostreoidea | 0.70 | 1.37 | 1.26 | 0.68 | 4.27 | 5.65 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 13 | Bellucina semperiana | 0.64 | 0.71 | 0.52 | 0.97 | 0.00 | 0.13 | 10.66 | 22.44 | 0.20 | 34.36 | 31.91 | 0.99 | 0.75 |
| 14 | Cavilucina fieldingi | 0.59 | 0.79 | 0.84 | 1.34 | 0.00 | 0.26 | 0.03 | 1.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 15 | Divaricella macandrewae | 0.22 | 0.00 | 0.10 | 0.37 | 0.00 | 0.00 | 1.90 | 8.86 | 0.20 | 8.30 | 5.79 | 0.08 | 0.04 |
| 16 | Rastafaria sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.22 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 17 | Pillucina fischeriana | 3.00 | 3.35 | 4.29 | 4.36 | 0.00 | 0.56 | 0.87 | 0.00 | 0.05 | 0.25 | 0.00 | 0.00 | 0.00 |
| 18 | Wallucina erythraea | 5.19 | 5.48 | 6.55 | 7.03 | 0.23 | 2.74 | 2.22 | 2.13 | 0.00 | 1.90 | 0.48 | 0.00 | 0.00 |
| 19 | Chamoidea gen. et sp. indet | 0.00 | 0.05 | 0.37 | 0.24 | 1.72 | 0.56 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 20 | Cardites akabana | 0.10 | 0.09 | 0.58 | 0.12 | 0.00 | 0.04 | 2.30 | 16.95 | 0.00 | 0.00 | 0.29 | 0.00 | 0.00 |
| 21 | Fragum nivale | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.19 | 0.00 | 0.00 | 0.00 | 0.00 |
| 22 | Parvicardium sueziensis | 7.68 | 9.01 | 10.25 | 9.27 | 0.00 | 0.30 | 4.74 | 0.17 | 7.16 | 0.13 | 0.00 | 0.04 | 0.00 |
| 23 | Tellina lactea | 5.39 | 7.20 | 9.10 | 8.18 | 0.00 | 2.43 | 0.40 | 1.16 | 0.00 | 0.27 | 0.00 | 0.00 | 0.00 |
| 24 | Tellina flacca | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.80 | 1.83 | 5.95 | 5.95 |
| 25 | Abra sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.55 | 0.00 | 0.89 | 0.10 | 0.15 | 0.13 |
| 26 | Ervilia scaliola | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 2.19 | 0.00 | 0.00 | 0.00 | 0.00 |
| 27 | Semele fragillima | 2.04 | 3.49 | 2.77 | 3.15 | 0.00 | 0.52 | 1.54 | 2.65 | 3.18 | 1.52 | 0.00 | 0.19 | 0.22 |
| 28 | Leptomyaria sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 7.61 | 8.65 | 0.72 | 1.20 |
| 29 | Callista florida | 1.51 | 2.52 | 5.70 | 3.64 | 0.00 | 0.00 | 1.41 | 0.01 | 0.20 | 0.13 | 0.10 | 0.04 | 0.04 |
| 30 | Costellipitar chordata | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.83 | 3.51 |
| 31 | Microcirce sp. | 0.00 | 0.71 | 0.00 | 0.00 | 0.11 | 0.00 | 0.39 | 6.38 | 0.00 | 18.89 | 25.28 | 3.71 | 2.97 |
| 32 | Redicirce sulcata | 1.03 | 0.62 | 0.63 | 1.27 | 0.00 | 0.00 | 3.37 | 1.69 | 0.00 | 0.40 | 2.51 | 0.00 | 0.00 |
| 33 | Timoclea roemeriana | 0.05 | 0.13 | 0.21 | 0.12 | 0.00 | 0.04 | 0.17 | 0.21 | 0.00 | 1.14 | 0.87 | 0.00 | 0.00 |
| 34 | Corbula erythraeensis | 0.00 | 0.00 | 0.00 | 0.00 | 0.34 | 0.00 | 0.00 | 0.58 | 0.00 | 2.41 | 2.31 | 18.01 | 13.14 |
| 35 | Patelloida spp. | 1.26 | 1.54 | 0.68 | 0.91 | 2.83 | 2.26 | 0.01 | 0.00 | 0.80 | 0.00 | 0.10 | 0.00 | 0.00 |
| 36 | Phasianella spp. | 1.38 | 0.35 | 0.47 | 0.18 | 0.00 | 0.00 | 0.26 | 0.41 | 0.00 | 0.13 | 0.00 | 0.00 | 0.00 |
| 37 | Obtusella cf. tiberiana | 1.38 | 2.56 | 1.46 | 0.79 | 0.00 | 0.17 | 5.85 | 0.00 | 0.80 | 0.25 | 0.58 | 0.15 | 0.40 |
| 38 | Pagodatrochus veriabilis | 1.40 | 1.46 | 1.78 | 1.33 | 0.00 | 0.04 | 5.23 | 0.71 | 0.40 | 0.25 | 0.38 | 0.00 | 0.00 |
| 39 | Perrinia stellata | 0.00 | 0.00 | 0.00 | 0.24 | 0.00 | 0.00 | 1.20 | 0.77 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 40 | Pseudominolia nedyma | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 1.14 | 0.97 | 13.19 | 13.00 |
| 41 | Trochidae gen. et sp. indet 1 | 1.43 | 0.49 | 0.05 | 0.18 | 0.00 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.04 |
| 42 | Bothropoma cf. munda | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.04 | 0.29 | 3.22 | 0.00 | 0.51 | 0.67 | 0.00 | 0.00 |
| 43 | Collonista arsinoensis | 0.00 | 0.04 | 0.00 | 0.06 | 1.02 | 1.35 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 44 | Pisulina adamsiana | 0.00 | 0.00 | 0.00 | 0.00 | 2.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 45 | Smaragdia spp. | 0.89 | 0.79 | 0.94 | 0.58 | 0.00 | 0.13 | 8.42 | 3.40 | 0.80 | 0.89 | 0.48 | 0.00 | 0.00 |
| 46 | Peasiella spp | 1.01 | 0.35 | 0.73 | 0.55 | 0.00 | 0.00 | 0.00 | 0.00 | 1.39 | 0.00 | 0.00 | 0.00 | 0.00 |
| 47 | Rissoina spp. | 7.31 | 5.69 | 3.87 | 3.88 | 17.00 | 28.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 48 | Stosicia sp. | 0.00 | 0.00 | 0.00 | 0.00 | 1.36 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 49 | Cerithium zebrum | 0.02 | 0.09 | 0.10 | 0.06 | 2.49 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 50 | Cerithium egenum | 0.27 | 0.49 | 0.05 | 0.55 | 1.59 | 2.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 51 | Cerithium rostratum | 0.59 | 0.18 | 0.00 | 0.24 | 0.00 | 0.00 | 1.20 | 1.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 52 | Clypeomorus cf. brevis | 1.21 | 0.18 | 0.47 | 0.42 | 0.00 | 0.00 | 0.00 | 0.00 | 15.12 | 0.00 | 0.00 | 0.00 | 0.00 |
| 53 | Plesiotrochus souverbianus | 0.30 | 0.97 | 0.26 | 0.36 | 4.19 | 1.35 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 54 | Rhinoclavis sordidula | 0.00 | 0.18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.38 | 0.00 | 18.16 | 17.04 |
| 55 | Diala spp. | 7.21 | 8.03 | 5.28 | 5.63 | 2.61 | 4.04 | 15.71 | 3.98 | 3.38 | 0.51 | 1.73 | 0.00 | 0.04 |
| 56 | Fenella cf. diplax | 1.80 | 0.00 | 0.42 | 0.00 | 0.11 | 0.96 | 1.17 | 0.03 | 0.00 | 5.32 | 7.69 | 6.48 | 10.47 |
| 57 | Styliferina cf. goniochila | 0.20 | 0.35 | 0.05 | 0.06 | 0.00 | 0.09 | 1.71 | 0.00 | 0.00 | 0.25 | 0.00 | 0.00 | 0.00 |
| 58 | Obtortio cf. pupoides | 0.20 | 0.00 | 0.21 | 0.00 | 0.00 | 0.04 | 0.52 | 0.00 | 0.00 | 2.66 | 2.60 | 3.83 | 6.35 |
| 59 | Potamides conicus | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 38.17 | 0.00 | 0.00 | 0.00 | 0.00 |
| 60 | Hipponix conicus | 0.34 | 0.26 | 0.26 | 1.15 | 4.20 | 3.43 | 0.44 | 3.93 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 |
| 61 | Hipponix sp. 2 | 0.00 | 0.00 | 0.00 | 0.00 | 2.72 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 62 | Natica sp. 1 juv. | 0.71 | 0.00 | 0.21 | 0.00 | 0.11 | 0.26 | 0.00 | 0.01 | 0.80 | 0.25 | 0.00 | 0.80 | 1.11 |
| 63 | Buccinidae gen. et sp. indet. 1 | 0.39 | 0.00 | 0.63 | 0.24 | 2.04 | 1.48 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 64 | Anachis exilis | 0.02 | 0.26 | 0.10 | 0.06 | 0.00 | 0.00 | 4.13 | 0.87 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 |
| 65 | Euplica ionida | 2.68 | 1.24 | 0.37 | 1.39 | 1.13 | 1.61 | 0.78 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 66 | Zafra cf. selasphora | 0.00 | 0.40 | 0.10 | 0.00 | 0.91 | 1.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 67 | Zafrona isomella | 0.39 | 0.79 | 0.05 | 0.85 | 7.37 | 2.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 68 | Coralliophila spp. | 0.64 | 0.31 | 0.10 | 0.67 | 1.48 | 1.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 69 | Gibberula spp. | 1.99 | 1.28 | 0.42 | 1.51 | 0.57 | 1.48 | 1.33 | 0.69 | 6.37 | 0.00 | 0.00 | 0.00 | 0.00 |
| 70 | Nassarius cf. delicatus | 2.98 | 3.00 | 1.36 | 1.58 | 0.00 | 0.82 | 0.30 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 71 | Nassarius cf. hameroessa | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.38 | 0.19 | 2.92 | 2.13 |
| 72 | Ancilla sp. | 0.22 | 0.44 | 1.31 | 0.36 | 0.00 | 0.13 | 0.33 | 0.14 | 0.00 | 0.13 | 0.00 | 0.00 | 0.04 |
| 73 | Ceritoturris sp. | 2.58 | 1.46 | 0.47 | 1.94 | 0.79 | 6.73 | 0.00 | 0.52 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 74 | Clavus spp. | 0.47 | 0.09 | 0.68 | 0.12 | 0.23 | 0.04 | 0.02 | 0.02 | 1.19 | 0.00 | 0.00 | 0.00 | 0.00 |
| 75 | Cerithiopsidae | 0.22 | 0.71 | 0.47 | 0.12 | 1.25 | 0.78 | 0.39 | 0.17 | 0.00 | 0.25 | 0.00 | 0.00 | 0.00 |
| 76 | Triphoridae | 0.32 | 0.44 | 0.37 | 0.73 | 12.58 | 4.95 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 77 | Eulimidae | 0.22 | 0.53 | 0.47 | 0.73 | 0.45 | 1.35 | 0.39 | 0.01 | 0.00 | 0.00 | 0.00 | 0.08 | 0.18 |
| 78 | Chrysallida spp. | 1.28 | 0.84 | 1.10 | 1.21 | 0.00 | 0.30 | 1.57 | 0.17 | 0.00 | 0.00 | 0.19 | 0.08 | 0.18 |
| 79 | Odostomia spp. | 0.47 | 1.02 | 1.20 | 0.91 | 0.00 | 0.17 | 2.34 | 0.69 | 0.20 | 0.00 | 0.00 | 0.00 | 0.04 |
| 80 | Pyramidella spp | 1.38 | 0.26 | 0.84 | 0.24 | 0.00 | 0.09 | 0.14 | 0.01 | 0.22 | 0.00 | 0.00 | 0.00 | 0.00 |
| 81 | Syrnola s.l. spp | 0.47 | 0.26 | 0.84 | 1.03 | 0.00 | 0.17 | 0.79 | 0.35 | 1.99 | 0.51 | 0.38 | 0.00 | 0.00 |
| 82 | Turbonilla spp. | 0.42 | 0.62 | 0.89 | 1.51 | 0.11 | 0.13 | 4.55 | 0.35 | 0.20 | 0.76 | 0.77 | 0.11 | 0.22 |
| 83 | Atys cf. cylindrica | 0.25 | 0.04 | 0.26 | 0.06 | 0.00 | 0.04 | 0.03 | 0.02 | 1.39 | 0.51 | 0.00 | 0.64 | 0.80 |
| 84 | Haminoea sp. 1 | 0.30 | 1.59 | 1.31 | 1.03 | 0.00 | 0.09 | 0.02 | 0.35 | 0.20 | 0.00 | 0.00 | 0.72 | 0.89 |
| 85 | Haminoea sp. 2 | 0.96 | 0.18 | 0.47 | 0.18 | 0.00 | 0.22 | 0.02 | 0.04 | 0.00 | 0.63 | 0.77 | 5.12 | 4.53 |
| 86 | Bulla sp. juv. | 0.00 | 0.04 | 0.10 | 0.06 | 0.11 | 0.00 | 1.17 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 87 | Mamilloretusa ? sp. | 0.89 | 1.10 | 1.36 | 0.79 | 0.00 | 0.96 | 0.00 | 0.00 | 0.00 | 0.13 | 0.00 | 0.00 | 0.00 |
| 88 | Tornatina inconspicua | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.51 | 0.38 | 8.98 | 9.54 |
| 89 | Retusa sp. 2 | 0.39 | 1.46 | 1.10 | 1.45 | 0.00 | 0.13 | 1.95 | 0.17 | 0.60 | 0.25 | 0.67 | 0.04 | 0.04 |
| 90 | Ringicula sp. 1 | 2.34 | 1.46 | 1.78 | 1.82 | 0.00 | 0.09 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 91 | Ringicula sp. 2 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.64 | 0.52 | 0.00 | 0.38 | 0.00 | 1.25 | 1.29 |
| 92 | Tornatina sp.1-3 | 1.85 | 2.16 | 2.30 | 2.42 | 0.23 | 0.69 | 0.13 | 0.00 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 |
| 93 | Siphonaria sp. 2 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 4.18 | 0.00 | 0.00 | 0.00 | 0.00 |
| 94 | Gadila sp. | 1.48 | 2.12 | 2.14 | 2.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 0.00 | 0.00 | 0.00 |
| 95 | Polyschides sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.30 | 3.20 |
| 96 | Polyplacophora | 0.12 | 0.13 | 0.10 | 0.30 | 2.61 | 3.26 | 0.00 | 0.00 | 0.60 | 0.00 | 0.00 | 0.00 | 0.00 |
| | total % | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 | 100.00 |

Tab. 9. Percentage of taxa (reduced data set) in samples.

| taxa | feeding strategy | relation to substrate |
|---|---|---|
| Nucula inconspicua | deposit-feeder | burrowing |
| Huxleya diabolica | deposit-feeder | burrowing |
| Acar plicata | suspension feeder | bysally attached |
| Barbatia spp. | suspension feeder | bysally attached |
| Limopsis sp. | suspension feeder | burrowing |
| Glycymeris spp. | suspension feeder | burrowing |
| Brachidontes variabilis | suspension feeder | bysally attached |
| Septifer sp. | suspension feeder | bysally attached |
| Crenella striatissima | suspension feeder | bysally attached |
| Spondylidae | suspension feeder | cemented |
| Anomioidea | suspension feeder | cemented* |
| Ostreoidea | suspension feeder | cemented |
| Bellucina semperiana | chemosymbionts | burrowing |
| Cavilucina fieldingi | chemosymbionts | burrowing |
| Divaricella macandrewae | chemosymbionts | burrowing |
| Rastafaria calypso | chemosymbionts | burrowing |
| Pillucina fischeriana | chemosymbionts | burrowing |
| Wallucina erythraea | chemosymbionts | burrowing |
| Chamoidea gen. et sp. indet | suspension feeder | cemented |
| Cardites akabana | suspension feeder | burrowing |
| Fragum nivale | suspension feeder | burrowing |
| Parvicardium sueziensis | suspension feeder | burrowing |
| Tellina lactea | deposit-feeder | burrowing |
| Tellina flacca | deposit-feeder | burrowing |
| Abra sp. | deposit-feeder | burrowing |
| Ervilia scaliola | deposit-feeder | burrowing |
| Semele fragillima | deposit-feeder | burrowing |
| Leptomyaria sp. | deposit-feeder | burrowing |
| Callista florida | suspension feeder | burrowing |
| Costellipitar chordata | suspension feeder | burrowing |
| Microcirce miliacea | suspension feeder | burrowing |
| Redicirce sulcata | suspension feeder | burrowing |
| Timoclea roemeriana | suspension feeder | burrowing |
| Corbula erythraeensis | suspension feeder | burrowing |

Tab. 10. Feeding strategies (after Morton 1983 and Le Pennec et al. 1995) and relations to substrate (after Oliver 1992) of bivalve taxa. * = simplified substrate relation for Anomoidea.

## Discussion
### Faunal associations

The faunal associations are composed of a large number of taxa, for most of which information as to habitat preferences have been unknown until now. Some of these taxa are definitely new records for the Red Sea and some are probably new to science (Glover & Taylor, 1997; Zuschin & Oliver, submitted).

After data reduction (mostly based on relative abundances within samples), most of the remaining taxa contribute a substantial quantitative amount of the total fauna considered in the statistical analyses. A few taxa from the mangrove are of low quantitative importance because this sample contains by far the fewest number of individuals. The importance of Ervilia scaliola and Fragum nivale for characterizing the mangrove (or a transition from the mangrove to sand between coral patches) is thus very questionable, and these taxa are consequently not considered. The various cluster analyses convey a consistent strong

| Factor | Eigenvalue | Percentage of variance | Cumulative Percentage |
|---|---|---|---|
| 1 | 4.43660 | 34.1 | 34.1 |
| 2 | 3.32590 | 25.6 | 59.7 |
| 3 | 1.99060 | 15.3 | 75.0 |
| 4 | 1.55997 | 12.0 | 87.0 |
| 5 | 0.80356 | 6.2 | 93.2 |
| 6 | 0.39771 | 3.1 | 96.3 |
| 7 | 0.26345 | 2.0 | 98.3 |
| 8 | 0.14282 | 1.1 | 99.4 |
| 9 | 0.04353 | 0.3 | 99.7 |
| 10 | 0.01545 | 0.1 | 99.8 |
| 11 | 0.01004 | 0.1 | 99.9 |
| 12 | 0.00620 | 0.0 | 100.0 |
| 13 | 0.00416 | 0.0 | 100.0 |

Tab. 12. Percentages explained by the 13 factors of factor analysis using bivalves only.

| sample | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|---|---|---|---|---|
| 1 | 0.975 | -0.016 | -0.062 | 0.017 |
| 2 | 0.991 | -0.016 | -0.071 | -0.007 |
| 3 | 0.981 | -0.043 | -0.076 | -0.024 |
| 4 | 0.989 | -0.014 | -0.075 | -0.021 |
| 5 | -0.100 | 0.952 | 0.120 | -0.026 |
| 6 | -0.120 | 0.918 | 0.134 | -0.022 |
| 7 | -0.088 | 0.019 | 0.986 | -0.045 |
| 8 | -0.106 | 0.017 | 0.987 | -0.057 |
| 9 | -0.088 | -0.152 | -0.108 | 0.869 |
| 10 | 0.328 | -0.103 | -0.169 | -0.464 |
| 11 | 0.276 | -0.109 | -0.119 | 0.863 |
| 12 | 0.353 | 0.829 | -0.117 | -0.135 |
| 13 | -0.113 | 0.874 | -0.093 | -0.056 |

Tab. 13. Loadings of samples by factors 1-4 of the rotated factor matrix using bivalves only.

| Factor | Eigenvalue | Percentage of variance | Cumulative Percentage |
|---|---|---|---|
| 1 | 4.91368 | 37.8 | 37.8 |
| 2 | 2.82008 | 21.7 | 59.5 |
| 3 | 1.80506 | 13.9 | 73.4 |
| 4 | 1.03846 | 8.0 | 81.4 |
| 5 | 0.99075 | 7.6 | 89.0 |
| 6 | 0.73817 | 5.7 | 94.7 |
| 7 | 0.28992 | 2.2 | 96.9 |
| 8 | 0.15582 | 1.2 | 98.1 |
| 9 | 0.10613 | 0.8 | 98.9 |
| 10 | 0.07107 | 0.5 | 99.5 |
| 11 | 0.04943 | 0.4 | 99.8 |
| 12 | 0.01885 | 0.1 | 100.0 |
| 13 | 0.00259 | 0.0 | 100.0 |

Tab. 14. Percentages explained by the 13 factors of factor analysis using gastropods only.

| life habits | sand between coral patches | | | | muddy sand | | mud | | reef slope | | mangr. | seagrass | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 11 | 10 | 12 | 13 |
| burrowing chemosymbionts | 21.37 | 19.99 | 20.58 | 24.39 | 54.07 | 47.16 | 3.10 | 2.80 | 0.89 | 15.48 | 2.13 | 46.44 | 46.90 |
| burrowing deposit feeders | 17.82 | 24.67 | 22.32 | 22.59 | 18.07 | 14.13 | 21.84 | 28.26 | 0.00 | 13.84 | 25.56 | 7.80 | 14.05 |
| burrowing suspension feeders | 48.93 | 45.42 | 48.64 | 45.42 | 27.86 | 38.71 | 74.94 | 68.79 | 5.35 | 12.38 | 41.66 | 44.32 | 33.99 |
| bysally attached suspension feeders | 10.05 | 7.00 | 5.67 | 5.89 | 0.00 | 0.00 | 0.11 | 0.16 | 48.52 | 29.14 | 30.65 | 1.44 | 5.04 |
| cemented suspension feeders | 1.84 | 2.91 | 2.80 | 1.70 | 0.00 | 0.00 | 0.00 | 0.00 | 45.23 | 29.16 | 0.00 | 0.00 | 0.01 |

Tab. 11. Percentage of bivalve life habits in samples.

| sample | Factor1 | Factor2 | Factor3 | Factor4 |
|--------|---------|---------|---------|---------|
| 1 | 0.615 | 0.701 | 0.092 | -0.002 |
| 2 | 0.753 | 0.602 | -0.048 | 0.019 |
| 3 | 0.761 | 0.534 | 0.004 | -0.011 |
| 4 | 0.741 | 0.590 | -0.072 | -0.027 |
| 5 | 0.001 | -0.064 | 0.972 | 0.164 |
| 6 | 0.112 | 0.000 | 0.977 | 0.081 |
| 7 | -0.142 | -0.117 | 0.271 | 0.919 |
| 8 | -0.149 | -0.108 | 0.436 | 0.862 |
| 9 | -0.104 | 0.856 | -0.086 | -0.039 |
| 10 | -0.049 | -0.069 | 0.088 | -0.346 |
| 11 | 0.062 | 0.938 | -0.025 | 0.021 |
| 12 | 0.898 | -0.096 | 0.118 | -0.038 |
| 13 | 0.705 | -0.157 | 0.015 | -0.076 |

Tab. 15. Loadings of samples by factors 1-4 of the rotated factor matrix using gastropods only.

dependence of associations on sedimentary facies and slightly varying relations between associations: The seagrass associations mark a transition from sand between coral patches to muddy sand as far as absolute frequencies of taxa are concerned. They are closely related to muddy sand associations with respect to bivalve life habits, but show similar high individual numbers, numbers of taxa and diversity indices as associations from sand between coral patches and reef slopes. The mangrove association in contrast is related to associations in sand between coral patches with respect to taxonomic composition and bivalve life habits, but shows similar low individual numbers, numbers of taxa and diversity indices as the muddy sand and mud associations.

The correspondence analysis supports the results of the cluster analyses in that it confirms the relationships between seagrass bivalves and the muddy sand fauna, and between seagrass gastropods and those in sand between coral patches. As far as absolute frequencies of taxa along with the state of preservation and ontogenetic condition is concerned, the allocation of some taxa to sedimentary facies has to be slightly modified: For example, adult and well-preserved individuals of *Cerithium rostratum* and *Phasianella* spp. occur preferentially in the two seagrass samples, *Bothropoma* cf. *munda* occurs preferentially in the muddy seagrass sample. These taxa are therefore interpreted to have a stronger relation to the respective facies than indicated by the statistical analysis. In the case of *Bothropoma* cf. *munda*, the strong relation to muddy seagrass is additionally supported by large numbers of their typical opercula, which contribute considerably to the finer sediment fraction of this sample.

## Ecological aspects

The associations are not only very distinct with respect to absolute frequencies of taxa, numbers of taxa and individual numbers, but also with respect to ecological features such as diversity or life habits of bivalves.

In none of the associations does one of the taxa dominate so clearly, that it can be considered as the trophic nucleus (as defined by ANTIA, 1977). In three associations, their characteristic taxa coincide with the prevalent taxa:
*"Rhinoclavis sordidula - Corbula erythraeensis - Pseudominolia nedyma* association" from the mud facies;
*"Glycymeris* spp. *- Parvicardium sueziensis - Diala* spp. association" from sand between coral patches;
*"Rissoina* spp. - Triphoridae - Ostreoidea association" from reef slopes.

In contrast, the associations from muddy sand (*"Microcirce* sp. *- Leptomyaria sp.* association"), muddy seagrass (*"Crenella striatissima - Rastafaria calypso - Cardites akabana* association") and sandy seagrass (*"Smaragdia* spp. *- Perrinia stellata - Anachis exilis* - association") are characterized by taxa which are not or only partly prevalent taxa. Rather, these three associations have strong mutual transitions, best indicated by the very abundant *Bellucina semperiana*, which is a prevalent taxon in all three associations. The association from the mangrove channel (*"Potamides conicus* and *Siphonaria* sp. 2 - association") shows transitions to sands between coral patches, which are best indicated by the prevalent taxon *Clypeomorus* cf. *brevis*

Of all associations, the one from mud (*"Rhinoclavis sordidula - Corbula erythraeensis - Pseudominolia nedyma* association") is most distinct in its taxonomic composition: it shows only minor similarities to other associations.

The allocation of taxa to sedimentary facies is very well explained by the first 6 dimensions extracted by correspondence analysis and the first 4 factors of factor analysis including bivalves only. All of these factors are interpreted to emphasize special ecological conditions:

A. Correspondence analysis: Dimension 1 is interpreted as an "energy factor", which separates the sample sites with low water energy and finer grain size (mud, muddy sand, muddy sand with seagrass) from sites with higher water energy and coarse-grained sediments (reef slope, sand between coral patches, sandy seagrass, mangrove). Dimension 2 is interpreted as a "mud factor" because it distinctly separates the samples from mud from all other fine-grained sedimentary facies. This factor could be a combination of very fine sediment, very low water energy and minor sediment compaction. Dimension 3 is interpreted

| facies | sand between coral patches | | | | muddy sand | | mud | | reef slope | | mangr. | seagrass | | |
|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 11 | 10 | 12 | 13 | total |
| total mollusc content | 783335 | 726466 | 565910 | 404645 | 208712 | 299624 | 35904 | 28168 | 224282 | 592774 | 21120 | 462832 | 68349 | 4422121 |
| number of fragments | 704847 | 638948 | 492743 | 340873 | 194893 | 281077 | 24912 | 18520 | 191649 | 504448 | 16441 | 434814 | 57031 | 3901196 |
| number of individuals | 78488 | 87518 | 73167 | 63772 | 13819 | 18547 | 10992 | 9648 | 32633 | 88326 | 4679 | 28018 | 11318 | 520925 |
| % fragments | 89.98 | 87.95 | 87.07 | 84.24 | 93.38 | 93.81 | 69.39 | 65.75 | 85.45 | 85.10 | 77.85 | 93.95 | 83.44 | 88.22 |
| % individuals | 10.02 | 12.05 | 12.93 | 15.76 | 6.62 | 6.19 | 30.61 | 34.25 | 14.55 | 14.90 | 22.15 | 6.05 | 16.56 | 11.78 |

Tab. 16. Number and percentage of whole individuals and fragments of samples.

as a "mangrove factor" because it separates the mangrove channel from all other sedimentary facies. This factor might be a combination of extreme environmental conditions (e.g., strong variations in temperature and salinity) and a high supply of particulate organic matter provided by the mangrove plants. Dimension 4 is difficult to interpret with regard to samples; considering taxa also, dimension 4 can be interpreted as an "environment factor of reef slopes and the mangrove": taxa showing significant loadings have strong restrictions to these sedimentary facies, are very well suited to characterize it (especially in contrast to the association from sand between coral patches) and are therefore interpreted to emphasize its environment conditions. Dimension 5 is interpreted as a "seagrass factor", because it separates this sedimentary facies from all others. The occurrence of taxa showing high loadings is primarily dependent on the occurrence of seagrass. In contrast, dimension 6 is interpreted as a "discriminating factor within seagrass", because it separates sandy seagrass and muddy seagrass. The reasons for this might be differences in water energy, grain size, seagrass density or taxonomic seagrass composition at the two sites.

B. Factor analysis on bivalve samples: Factor one of the factor analysis based on bivalves correlates with the large amount of burrowing suspension feeders in sand between coral patches. This factor is therefore interpreted to summarize substrate preferences for coarse-grained sediments and sufficient suspension load in the water column. Factor 2 correlates with the dominance of infaunal chemosymbionts and deposit-feeders in muddy sands and seagrass and is interpreted to reflect a substrate preference for strongly compacted soft bottoms with high organic enrichment. Factor 3 correlates with the dominance of infaunal suspension-feeders in mud and probably summarizes the substrate preference for very poorly compacted soft bottoms and for a nutrient rich water column.

Factor 4 correlates with the dominance of epifaunal (byssate and cemented) suspension feeders on reef slopes and is interpreted to reflect primarily the preference for hard substrates but also for sufficient food supply in the water column.

Overall, bivalve life habits show a strong dependence on sedimentary facies, which can be attributed to strong correlation between substrates and feeding strategies. In contrast a generalization of feeding strategies and even substrate relations cannot be done for gastropods because only limited information is available on the ecology (e.g., TAYLOR & REID, 1984) of many taxa. This is especially true for most microgastropods and particularly for the abundant opisthobranchs (KOHN, 1983). Even for seemingly well known groups like trochids, a generalization is very questionable: most authors consider them to be algal grazers, but there is strong evidence that at least some trochids feed as grazing predators on hydroids and other sessile invertebrates (e.g., PERRON, 1975) and the members of the subfamily Umboniinae, like *Pseudominolia nedyma*, are known for their suspension-feeding mode of life (e.g. FRETTER, 1975; HICKMAN, 1985).

For some important gastropod taxa, however, information on feeding strategies can be provided: On reef slopes, triphorids, which are parasitic on sponges (Marshall 1983), and rissoids, which feed on algal-filaments and diatoms (PONDER, 1985), are very important. In sand between coral patches, the dialids, closely related to cerithiids, are most likely algal-detritus feeders, as are the abundant *Smaragdia* spp. in seagrass (KAY, 1979). In the mangrove, *Potamides conicus* probably feeds on particulate organic matter (BOSCH et al., 1995) provided by the mangrove plants. In mud, the very abundant *Rhinoclavis sordidula* are well known algal-detritus feeders (HOUBRICK, 1978).

All in all, the gastropod life habits tend to show a facies-dependent distribution; because gastropods are predominantly vagile, this dependence probably reflects feeding strategies more than substrate relations.

Taphonomic and palaeoecological aspects

We believe that the associations (death assemblages) are produced by the local fauna because they correlate so strongly with sedimentary facies, and because there is no sedimentological evidence for considerable transport that would produce allochthonous assemblages (compare also NEBELSICK, 1992b). Moreover, the ecological properties of the associations match so well with the sedimentary facies, that the species distributions are very unlikely a consequence of the behavior of shells as sedimentary particles. We have no data on the time-scale (sensu FÜRSICH & ABERHAN, 1990) or significance (sensu KOWALEWSKI, 1996) of time-averaging of the death assemblages. They may be simple parautochthonous assemblages (sensu KIDWELL et al., 1986) of a few generations, which probably would yield a more accurate picture of the whole benthic molluscan community than one-time observations of the life assemblages (e.g., EKDALE, 1977; CARTHEW & BOSENCE, 1986), because of the short-term fluctuations and patchy distributions characteristic of life benthic communities (McCALL & TEVESZ, 1983). Or it may also be a multi-habitat time averaged assemblage (sensu KIDWELL & BOSENCE, 1991) from ecologically distinct communities. Considering also data of NEBELSICK' s (1992b) investigation on echinoids in the Northern Bay of Safaga, insignificant short-term time-averaging seems to predominate: live and dead faunal elements show good correspondence and the taphonomic signatures of the fragments he investigated show only minor differences. Interpreting these data, the studied molluscan assemblages could reflect the original biocoenosis quite well. Unfortunately echinoids have comparitively fragile skeletons and are therefore certainly less prone to time-averaging than molluscs (KOWALEWSKI, 1997), for which long-term and significant time-averaging seems to be a universal occurrence (FLESSA ,1993; KIDWELL, 1993; FLESSA & KOWALEWSKI, 1994; MELDAHL et al., 1997).

However, due to time-averaging of the accumulating death assemblage (CARTHEW & BOSENCE, 1986), the original diversity of the preservable fauna tends to be overestimated

(e.g., ANTIA, 1977; STAFF et al., 1986), particularly in environmentally variable habitats (STAFF & POWELL, 1988). The sampled upper tens of centimeters of the sedimentary column is the taphonomically active zone, where most taphonomic processes (dissolution, fragmentation, disarticulation) take place and which contains the significantly or insignificantly, short-term or long-term, time-averaged parautochthonous death assamblage (FÜRSICH, 1978; POWELL et al., 1989; FÜRSICH & ABERHAN, 1990; KIDWELL & BOSENCE, 1991; FLESSA & KOWALEWSKI, 1994; KOWALEWSKI, 1996). Therefore the studied faunas are not considered to be the potential fossil assemblage, but rather associations where taphonomic disintegration is still ongoing. The number of fragments for example is much higher than the number of whole individuals, and different abundances in the various sedimentary environments were recognized. Our sampling method and post-collection transport (FLESSA et al., 1992) surely contributed to the high numbers of fragments. However, because the samples from mud, with the highest proportion of fragile specimens, have by far the lowest proportion of fragments, we are confident that postcollection effects are minor. The different abundances of fragments point to different taphonomic processes or at least to differences in the effectiveness of taphonomic processes in the studied environments, which thus affect the absolute frequencies of faunal composition. Shell breakage is well known from high-energy environments (for a review see KIDWELL & BOSENCE, 1991), but is also extremely common in low-energy habitats (POWELL et al., 1989) like the studied ones and occurs either at death, by predation, or after death when dissolution, abrasion, and transportation take their toll (POWELL & DAVIES, 1990). Some authors suggest that biogenic interactions (e.g., predation) considerably contribute to breakage (e.g., TREWIN & WELSH, 1976; VERMEIJ, 1983; MELDAHL & FLESSA, 1990; CADÉE, 1994). However, to reduce taphonomic losses like fragmentation, the studied fauna must be buried in the zone of accumulation, which contains a rather stable death assemblage (the long-term death assemblage sensu POWELL et al., 1989), perhaps a potential fossil assemblage.

The present study emphasizes the importance of micromolluscs for facies analyses of modern sediments. Other studies have shown that most shells in modern environments are generally neither large (e.g., SALAZAR-JIMENEZ et al., 1982) nor adult (e.g., CUMMINS et al., 1986). Moreover, small but numerically abundant species seem to be the (palaeo)persistent part of communities (POWELL & STANTON, 1995). Generally the preservation potential of molluscs is high, but due to size-selective taphonomic disintegration larger size classes and adults tend to be preserved preferentially in the death assemblage (CUMMINS et al., 1986; POWELL et al., 1992). The potential fossil assemblage thus should contain proportionally more large individuals than the short-term death assemblage studied here. These larger individuals preserve most of a community's biomass and palaeoproduction and are therefore of special palaeoecological interest (POWELL & STANTON, 1985; 1996). Studies providing data on dissolution rates, shell ages and processes responsible for shell preservation in modern

marine environments are rare: Some authors suggest that dissolution rates are usually high enough that nothing would be preserved in most habitats (ALLER, 1982; POWELL et al., 1989) and that physical reworking is usually necessary for shell net accumulation (DAVIES et al., 1989b). Others emphasize the great age of many shells at or near the surface (FLESSA & KOWALEWSKI, 1994; FLESSA et al., 1993) and the role of biogenic reworking for shell burial (MELDAHL, 1987; MYRICK & FLESSA, 1996). However, at least the number of species seems to be well preserved, because some individuals of nearly all preservable taxa are usually present in death assemblages of modern marine environments (e.g., WARME, 1969; STAFF et al., 1986), commonly even in correct rank order (review see KIDWELL & FLESSA, 1995)

Studies comparing modern marine molluscan assemblages with their neighbouring Pleistocene counterparts are also rare. Generally coral reef faunas in uplifted Pleistocene terraces along the Red Sea coast tend to be diagenetically reduced in numbers compared to modern sediments from the same area. The reduction of biota is due to the widespread vadose diagenetic environments in the Pleistocene sediments and is especially expressed for aragonitic molluscs (Dullo, 1983; 1984; 1990). The faunal reduction increases with age of the Pleistocene terraces and only thick-shelled *Tridacna* and *Strombus* shells are well preserved, whereas smaller shells are not recorded (Dullo, 1984). The diagenetic environment seems to govern shell preservation as the latter is very good (even primary colouration of molluscs is preserved) in uplifted terraces with slightly different climatic factors and geological settings along the Red Sea coast (Dullo, 1984). A comparison of Pleistocene and modern marine molluscan assemblages from coral reefs of the Kenya coast reveals significant faunal differences: surprisingly modern molluscan assemblages show a considerably lower species diversity, which is directly attributed to a marked reduction in habitat diversity due to sea-level changes since the late Pleistocene; the total species list, however, has been little altered (Crame, 1986). A good correspondence regarding numbers of taxa of modern and Pleistocene molluscs is also reported from the California coast, where living species not found as fossils are also rare today (VALENTINE, 1989).

Information on the occurrence of fossil micromolluscs is available not only for the Pleistocene, but also for older periods (e.g., JANSSEN, 1981; BANDEL, 1991b, 1993; Runnegar, 1996), and fossil micromolluscs have even been successfully used for facies and paleoecological analyses (STANTON et al., 1981; MAXWELL, 1988, 1992). Therefore we suspect that the poor state of knowledge on fossil smaller molluscs is not only due to a poor preservation potential; they are also largely ignored by both (paleo)malacology and micropalaeontology, which is typically restricted to foraminifers and ostracods.

## Conclusion

1. The sedimentary facies investigated here are not only characterized by distinct mollusc associations based on taxonomic composition; they show also clear differences

regarding descriptive features like individual abundance and numbers of taxa, taphonomic features like numbers of fragments, and ecological features such as diversity indices, feeding strategies and substrate relations.

2. The recognized associations are the result of mollusc distributions that reflect a variety of environmental parameters like water energy, grain size and food supply and are affected by taphonomic processes like fragmentation, which are variably efficient in the different environments.

3. The studied death assemblages probably do not reflect the original biocoenoses, but are rather long-term time-averaged assemblages from the taphonomically active zone. Therefore taphonomic processes continue to affect the death assemblages; to increase their preservation potential, they must be buried in the zone of accumulation.

4. The death assemblages from the taphonomically active zone provide an opportunity to quantify taphonomic loss by comparing them to long-term death assemblages from deeper parts of the sedimentary column and fossil assemblages from similar habitats. The number of species should be well preserved in fossil assemblages. The taphonomic loss of individual numbers in Pleistocene deposits must be cautiously assessed under consideration of the diagenetic environment and potential habitat changes due to sea-level fluctuations.

5. The poor state of knowledge on fossil micromolluscs is probably not only due to a rather low preservation potential; they are also largely ignored by both classical (palaeo)malacology and micropalaeontology.

## Acknowledgements

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